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Long-term Trends in Terrestrial and Marine Invertebrate Exploitation on the Eastern African Coast: Insights from Kuumbi Cave, Zanzibar

Patrick Faulkner[a,b]*, Matthew Harris[c], Othman Haji[d], Abdallah K. Ali[d], Alison Crowther[b,c], Ceri Shipton[e], Mark C. Horton[f], Nicole L. Boivin[b]

a. The University of Sydney, Faculty of Arts and Social Sciences, Department of Archaeology, Sydney, New South Wales, Australia

b. Max Planck Institute for the Science of Human History, Jena, Germany

c. School of Social Science, The University of Queensland, Brisbane, Australia

d. Department of Museums and Antiquities, Zanzibar, Tanzania

e. Centre of Excellence for Australian Biodiversity and Heritage, Australian National University, Canberra, Australia

f. Department of Archaeology and Anthropology, University of Bristol, Bristol, UK

*Correspondence to: patrick.faulkner@sydney.edu.au

Abstract

The nature and trajectory of coastal and maritime adaptations, and the complex ways foraging economies have been structured to include both marine and terrestrial resources, are becoming key topics of interest in African archaeological research. There is, therefore, an increasing need to understand the longer-term context for more recent shifts in coastal economies, and for greater attention to be paid to the role of a broader spectrum of resources. This is particularly the case for terrestrial and marine molluscs, which have been somewhat overlooked in discussions centred on past

economies in the region. The relative importance of these comparatively small-bodied faunal resources requires evaluation, particularly given their ubiquity within the archaeological record, and their potentially important contribution to dietary and economic practices. Kuumbi Cave, located in the southeast of Zanzibar (Unguja) Island, provides the ideal opportunity to investigate long-term trends in invertebrate use on the eastern African coast and islands. Here we discuss not only the trajectory of coastal resource exploitation and coastal economic adaptations in the region from the late Pleistocene, but also the significance of Kuumbi Cave as one of the few sites in eastern Africa that represents significant levels of exploitation of large terrestrial gastropods.

Keywords

Archaeomalacology; foragers; coastal adaptations; escargotières; coastal economy

Introduction

Given their ubiquity within the archaeological record of coasts, islands and other aquatic environments, shell midden deposits and molluscan remains have proved invaluable in furthering our understanding of human palaeoeconomies. As resources that have been exploited for at least 160,000 years, molluscs have been linked to aspects of human evolution and their foraging has been addressed in terms of the potential relationship to increasing behavioural complexity and the nature of human-environmental interactions (Bicho and Haws 2008; Marean 2010, 2014), the provision of key nutritional requirements (Kyriacou et al. 2015), and the incorporation of new symbolic or ideological dimensions to human culture (Jerardino and Marean 2010). Molluscs have also been used as critical evidence in advancing models of human population size shifts, shifting occupational intensity, and resource intensification (Jerardino 2012; Stiner and Munro 2011; Stiner et al. 2012). Finally, the increasingly sophisticated evaluation of molluscan assemblages with reference to detailed ecological and biological data for specific taxa has proven significant in evaluations of human-environment

interactions and potential resource depression (Braje et al. 2012; Erlandson et al. 2008; Giovas et al. 2010, 2013; Gutiérrez Zugasti 2011a). These examples highlight the value of molluscan resources in past economic structures and foraging strategies, and their potentially significant dietary role as a reliable and low risk dietary component (Erlandson 1988, 2001). Although undoubtedly important resources, however, the contribution of molluscs to past economies is unlikely to have followed a single pattern, and emphasis on molluscs probably varied considerably through time and space. One of the key issues in archaeomalacology, therefore, has been to address the specific role of molluscs and other invertebrate resources within palaeoeconomic strategies, assessing rather than assuming their relative importance as well as the question of whether they truly reflect secondary, fallback or low ranked resources (Colonese et al. 2011; see also Klein and Bird 2016).

This last point is of critical importance in the context of eastern African island and coastal archaeology. Mudida and Horton (1996:389), Fleisher (2003:354) and more recently Douglass (2016), have noted the limited information available for molluscs recovered from archaeological sites along the eastern African coast in comparison with terrestrial and marine vertebrates. Beyond a few notable exceptions (e.g. Douglass 2016; Faulkner et al. 2017; Fleisher 2003; Ichumbaki 2014; Msemwa 1994; Mudida and Horton 1996; Walz 2010a), this paucity of molluscan analyses in coastal eastern Africa reflects specific research priorities; namely a focus on Indian Ocean trade, urbanism and architecture, and detailed ceramic analyses (Wynne-Jones and Fleisher 2015). In fact, the broader body of research provides a robust framework for positioning detailed analyses of trends in molluscan exploitation. This is timely given the recent emphasis in eastern African archaeology on investigating the nature and trajectory of coastal and maritime adaptations (Crowther et al. 2016; Fleisher et al. 2015; Ichumbaki 2016), as well as resource use and conservation (e.g. Marchant and Lane 2014), and the need for greater consideration of the wider range of economic resources, including molluscs and other invertebrates.

These issues are not restricted to marine invertebrates, with terrestrial gastropods in prehistoric eastern Africa also used as subsistence resources and the shell modified for use as tools, implements and for decoration (e.g. Walz 2010a, 2016, 2017). Dense land snail deposits are known from many

regions around the world in both open and rockshelter or cave contexts, many of which date to the terminal Pleistocene to mid-Holocene (c. 12,000-5,000 BP). Possibly the best-known are the mounded escargotières associated with Capsian hunter-gatherers of the Mediterranean coast of North Africa (Lubell 2004a, 2004b; Lubell et al. 1976), but land snail middens are also distributed across southern Europe, southwestern Asia and the Levant (for a detailed synthesis see Lubell 2004b; also Gutiérrez Zugasti 2011b; Miracle 2001; Stiner and Munro 2011), as well as Southeast Asia (e.g. Rabett et al. 2011; Szabó et al 2003). Although terrestrial gastropods are commonly recovered from archaeological deposits across eastern Africa (particularly those within the family Achatinidae) and exploited to varying degrees at present (Walsh 2015; Walz 2010a, 2010b, 2016, 2017), dense land snail middens are comparatively rare. Some have been reported in mainland Tanzania, in the Manonga Valley (Harrison et al. 1997), at Mumba rockshelter (Mehlman 1979, 1989; Prendergast et al. 2007), and at Mlambalasi rockshelter (Biitner et al. 2017). Although a dense layer of land snail was noted in the excavation report from Mapangani (Makangale) Cave on Pemba Island (Chami et al. 2009:76), Kuumbi Cave on neighbouring Zanzibar (Unguja) Island represents the only site on the eastern African coast that at present contains significant deposits of land snail interpreted as being anthropogenic in origin (Chami 2009; Sinclair et al. 2006:103; Shipton et al. 2016).

Multiple phases of investigation at Kuumbi Cave (e.g. Chami 2009; Kourampas et al. 2015; Sinclair 2007; Sinclair et al. 2006; Shipton et al. 2016) have revealed a discontinuous sequence of occupation from the late Pleistocene to late Holocene, containing significant land snail and marine mollusc assemblages. Importantly, the initial research at Kuumbi Cave highlighted the prevalence of giant African land snail (*Achatina* spp.) through the sequence, in combination with indications of regularity in breakage patterns (linked to processing for meat extraction), and marine molluscs appearing in the mid-Holocene levels (Chami 2009; Sinclair 2007; Sinclair et al. 2006). Preliminary analyses of the invertebrate assemblages from more recent excavations (Shipton et al. 2016) indicates some differences in the initially reported trends, notably an older phase of marine mollusc exploitation during the terminal Pleistocene. As such, Kuumbi Cave provides the best opportunity to investigate

long-term diachronic trends in the exploitation of invertebrate resources, and potentially the trajectory of coastal adaptations, anywhere on the coast and islands of eastern Africa. Detailed description of the recently analysed fish (Shipton et al. 2016) and tetrapod (Prendergast et al. 2016; Shipton et al. 2016) assemblages indicate significant shifts in vertebrate faunal assemblage composition and diversity through time. Here we focus on detailed analyses of the invertebrate assemblage, building on the preliminary descriptions presented in Shipton et al. (2016). Like the recent work of Douglass (2016) and Faulkner et al. (2017) in Madagascar and Zanzibar respectively, the objectives here are to provide sufficient detail in a range of methods and analyses to provide an archaeomalacological foundation for further research in eastern Africa. We also highlight the taxonomic composition, richness and diversity of the Kuumbi Cave assemblage, offering new insights into the exploitation of invertebrates and the significance of these resources in the palaeoeconomic activities of the region.

Kuumbi Cave Location and Site Description

Kuumbi Cave is located in the Jambiani District on the southeastern portion of Zanzibar (Unguja) Island (Figure 1) and is one of several solutional caves within a series of Pleistocene-aged marine limestone terraces (Kourampas et al. 2015). Zanzibar Island was connected to the African mainland in the late Pleistocene, separating approximately 10,000 years ago during the period of post-glacial sea-level rise (Prendergast et al. 2016). Although only situated c. 2.5 km from the present-day coastline, because of the steep continental shelf off the eastern coast of the island, over the last 20,000 years the site would have been no more than 7-8 km from the shore (Prendergast et al. 2016; Shipton et al. 2016). The island has a wet/dry seasonal climate, although the eastern side is generally less humid, and characterised by shallow infertile soils covering coralline limestone bedrock (Juma 2004; Kourampas et al 2015). The vegetation across the Jambiani region is largely low scrubby bush due to the impoverished soils, but remnant tropical evergreen forest has been preserved around Kuumbi Cave,

probably representing part of the mosaic vegetation likely covering much of the island prior to disturbance via agricultural activity. Prendergast et al. (2016) have recently reviewed the sea level and palaeoenvironmental data for the southwestern Indian Ocean, with post glacial sea level rise increasing more rapidly in coastal eastern Africa after 12,000 BP, and in particular between 10-7,500 BP (at a rate of c. 12m/1000 years). This process effectively isolated Zanzibar as an island by 9-8,000 years ago. This pattern of sea level rise decreased from the early to mid-Holocene, with a local mid-Holocene highstand, to stabilise at present levels by approximately 3,000 BP, although there would appear to be multiple phases of sea level decrease (0.5-1 m below modern sea levels) followed by a more recent increase. On northwest Zanzibar, mangrove formation at 8,000 BP marks the end of the phase of rapid sea level rise, with broader observational data indicating a transition in mangrove composition and lower sea levels at 4,000 BP, coincident with increased climatic variability.

The results reported here arise from excavations at the site by the Sealinks Project in 2012, with detailed descriptions of the Kuumbi Cave Trench 10 stratigraphic sequence and dating provided in Kourampas et al. (2015) and Shipton et al. (2016). The deposit was excavated using the single context method, where each depositional (or stratigraphic) unit is treated as a single excavation unit, with 24 contexts in total identified through the sequence (Figure 2), including numerous hearths and cut/fill features not represented in the section. The excavated sediments were sieved through 3 mm mesh, with a minimum 60 litre bulk sediment sample taken from every context for flotation (0.3 mm mesh) and wet sieving (1 mm mesh). Those contexts representing less than 60 litres of excavated deposit were sampled in their entirety. Due to the high density and abundance of terrestrial molluscs in the Kuumbi sequence, a decision was made during excavation to sample the landsnail fauna via the flotation samples taken from each context. These recovery methods have some implications for structuring analyses of the invertebrates from Kuumbi Cave, for example, while the marine taxa were recovered from both the dry-sieved and flotation samples, the terrestrial molluscs were recovered almost exclusively via flotation sampling.

Four main chronological phases have been defined for Kuumbi Cave (Figure 2) based on geological, geomorphological and stratigraphic sequence data, and supported by a series of 20 radiocarbon and optically stimulated luminescence (OSL) dates obtained by the Sealinks Project (Kourampas et al. 2015; Prendergast et al. 2016; Shipton et al. 2016), which are summarised as follows. Phase 1 (contexts 1000-1011) broadly dates from the Late Iron Age (LIA, approx. 1-0.5 ka) to the Middle Iron Age (MIA, approx. 1.35-1 ka). Phase 2 (contexts 1015-1017) dates to the terminal Pleistocene-early Holocene transition (approx. 13-11 ka). No sediment layers were preserved for the intervening millennia between these two phases, likely because there was a hiatus in both cave occupation and sediment deposition. Kuumbi Cave, and perhaps the whole Island of Zanzibar, may have been abandoned in the early Holocene, concomitant with the early to mid-Holocene sea-level rise, and reoccupied in the Middle to Late Iron Age (Prendergast et al. 2016; Shipton et al. 2016). The main layers for Phase 3 (contexts 1018, 1019 and 1024) are late Pleistocene in age (approx. 19-17 ka). The latter part of Phase 3 is characterised by the erosion and then filling in (contexts 1020-1023) of a small channel that flowed around a large rock in the excavation, which may account for the intervening millennia between the main layers of Phases 2 and 3. Phase 4 (contexts 1025-1026) dates to before 20 ka. The latter phase does not contain clear, unambiguous evidence of human occupation through artefactual deposition, although the faunal material is at least suggestive of human activity. The relationship between these phases, the stratigraphic contexts (and their analytical grouping), the available chronologies linked to cultural deposition and the total/environmental sample volumes per unit that structure the following analyses are detailed in Table 1. The excavated volumes and age estimates in Table 1 indicate that sediment deposition took place at a rate of 0.297 litres per year in the main layers of Phase 3. There was an increase to 0.444 litres per year in Phase 2, and a notably more rapid rate of 2.178 litres per year in Phase 1. These rates of sediment deposition likely reflect increasing levels of human occupation with much of the sediment in these Phases derived from ash and other human inputs (Kourampas et al. 2015).

Methods

Invertebrate Identification, Quantification and Taphonomy

The Kuumbi Cave invertebrate assemblages were analysed at the House of Wonders Museum (Beit-el-Ajaib) in Stone Town, Zanzibar, with a preliminary recording and analysis undertaken in May 2013, and a second phase of data collection in November/December 2015. The preliminary invertebrate analyses have been reported in Shipton et al. (2016), and here we present the updated data from both the 2013 and 2015 study seasons. All invertebrate material has been re-classified and quantified, with some minor differences relative to the data presented in Shipton et al. (2016) due to taxonomic and quantitative revisions, and the incorporation of additional metrical data (particularly in the taxonomic attributions, MNI values and *Achatina* spp. size data). All material was identified to the lowest taxonomic level possible (predominantly species, genus or family) in comparison with published material (Abbott 1989; Abbott and Dance 1998; Bequaert 1951; Carpenter and Niem 1998; Richmond 2011; Robin 2008, 2011; Rowson 2007; Rowson et al. 2010; Spry 1964, 1968). Care was taken to avoid the over-identification of specimens, minimising the effects of over-estimating the contribution of taxa, such as those that are more robust and/or potentially more abundant. Where a fragment may have only retained morphological characteristics to family or genus level, it was not assumed that it was part of a dominant taxon already identified within the assemblage to species level (e.g. Szabó 2009:186; Woo et al. 2015:3). This is a critical issue for analyses aimed at understanding richness, diversity and comparative taxonomic contribution. All nomenclature has been standardised with reference to the World Register of Marine Species (WoRMS Editorial Board 2016).

Each taxon was quantified via calculation of the Minimum Number of Individuals (MNI). Due to the volume of material recovered from the Kuumbi Cave deposit and time constraints during analysis, the Number of Identifiable Specimens (NISP) and weight were unable to be recorded. As excavation of the site was undertaken stratigraphically, MNI has been calculated for each individual context (combining any arbitrary units within contexts) and summed per trench and/or chronological phase. Although

MNI is known to be significantly affected by aggregation (e.g. Grayson 1984:29-49; Lyman 2008:57-66), leading to an inflation in abundance estimates, each context from the Kuumbi Cave deposit represents a discrete depositional phase, and as such is seen to be the appropriate minimum analytical unit for MNI calculation. Based on the procedures outlined in Harris et al. (2015), MNI was recorded using a range of taxon-specific Non-Repetitive Elements (NRE). For bivalves, following siding to left and right valves, the range of NRE included the umbo and beak, the anterior and posterior portions of the hinge/dentition, and the anterior and posterior adductor muscle scars. Depending on shell morphology, the range of gastropod NRE comprised the spire, aperture, aperture lip, posterior and anterior canals, and the umbilicus. Further NRE used for specific gastropod taxa included the base and labum for the Cypraeidae, the columellar deck for the Neritidae, and the calcified opercula of the Turbinidae, Neritidae and Pomatiasidae. The chiton (Polyplacophora) NRE for MNI calculation was based on the highest counts of the apex of the anterior and mucro of the posterior valves (Giovas 2009:1560). Additionally, those specimens that were taxonomically identifiable but did not retain the necessary NRE for MNI calculation were noted as being present, and an MNI of 1 assigned per taxon for each individual context (e.g. Attenbrow 1992:20; Giovas 2009:1562; Jerardino and Marean 2010:413). To ensure independence of relative abundance data (i.e. avoiding multiple counts of individuals), MNI calculations per context were based on the NRE appropriate to the highest taxonomic level (family, genera or species), ensuring that individuals were not counted multiple times.

The general condition of the shell was noted for all samples, with the degree of fragmentation and burning assessed in a qualitative fashion and extent categorised as low (0-50%), moderate (50-75%) or high (75-100%). Any alteration to the marine shell by natural processes was also recorded, including beachrolling, boring and epibiont adhesions (such as worm-casts and barnacles) on the inner surfaces of the shell. There also are several other species known to prey on the Achatinidae, such as *Bdeogale tenuis* (Black-legged Mongoose), *Mungos mungo* (Banded Mongoose), rodents and terrestrial crabs (e.g. Kasigwa et al 1983:6; Williams 1951:305-306). Following permission from the Zanzibar Department of Forest and Non-Renewable Natural Resources, in collaboration with forest rangers

from Jozani Chwaka Bay National Park, 99 *Achatina* spp. specimens were collected from six sample locations as a comparative assemblage for identifying non-human shell modification.

Sample Size, Nestedness, Richness and Diversity

Species area curves and nestedness are used here to assess sample size and representativeness of the Kuumbi Cave assemblage (e.g. Lyman 2008, Peacock 2012, Peacock et al. 2012 and Wolverton et al. 2015). Species area curves are constructed by plotting the number of taxa (NTAXA) as a measure of taxonomic richness with sample size (MNI). As sample size increases, rare taxa should be progressively added, with sampling to redundancy achieved when no new taxa are included with any additional increase in sample size, reflected in an asymptotic curve (Lepofsky and Lertzman 2005; Lyman 2004, 2008; Lyman and Ames 2004). Nestedness will indicate whether samples with differing levels of taxonomic richness reflect subsets of each other. When drawn from the same community, faunal assemblages with lower richness should nest compositionally within those samples with higher richness. Nestedness temperature values (ranging between 0-100^{o}) provide a measure of this relationship, where 0^{o} represents a perfectly nested set of samples and 100^{o} represents no nestedness (Ulrich et al. 2009; Wolverton et al. 2015:502).

Several measures of richness and heterogeneity (following Magurran 1988) form the basis for the assessment of molluscan species diversity, richness and evenness through the Kuumbi Cave sequence. Variability in preservation within and between samples (e.g. fragmentation, weathering) has an impact on the occurrence of diagnostic features for identification, resulting in the attribution of specimens to different taxonomic levels. Taxonomic units were therefore grouped to the highest common level (e.g. family, genus) where appropriate to ensure independence in taxonomic classification for these analyses (Nagaoka 2000:100). The characteristics and performance of diversity statistics vary in terms of the variable being measured (richness, diversity/evenness), their sensitivity to sample size and discriminant ability. As such, there is value in using multiple indices to accurately

describe heterogeneity within and between samples (Magurran 1988:79). In addition to NTAXA to assess species richness, the Shannon index (*H*) and Simpson's index (1-*D*) are used to investigate diversity and dominance. All diversity indices were calculated using Palaeontological Statistics (PAST) version 3.13 (Hammer et al. 2001). Several other indices have been constructed to evaluate the proportional abundance of the dominant taxa and habitat areas. In combination with those measures highlighted above, these indices allow any trends in richness and diversity to be further explored, particularly in contrasting small, medium and large taxa from differing habitats. This broadly follows how similar indices have been calculated and evaluated within a foraging theory framework to evaluate aspects of foraging efficiency and potentially resource depression (e.g. Broughton 1994; Nagaoka 2000, 2002). The indices used here are the Land Snail index (∑Achatinidae/[∑Achatinidae + ∑Neritidae + ∑Turbinidae]); the *Nerita* spp. index (∑Neritidae/[∑Neritidae + ∑Turbinidae]); and the *Achatina reticulata* index (∑*A. reticulata*/[∑A. *reticulata* + ∑*Achatina fulica*]).

Achatina *spp. Size Estimation*

A series of measurements were taken on the *Achatina* spp. terrestrial snails as an additional possible means to differentiate between natural and cultural deposition, and to explore issues of potential size selectivity and foraging practices. Due to relatively high levels of fragmentation across all contexts, maximum shell lengths and widths could not be obtained on any of the *Achatina* spp. specimens. Measurements based on preserved landmarks were selected and applied to the assemblage for predicting original shell length (Figure 3). The regionally-specific independent control sample used to establish the morphometric equations comprised data on *Achatina* (*Lissachatina*) *allisa*, *Achatina* (*Lissachatina*) *fulica* agg., and *Achatina* (*Lissachatina*) *reticulata* shell length, shell width, aperture length and width from Zanzibar and Pemba published in Bequaert (1951:87, 127, 135). The same series of measurements, with the addition of columella length and body whorl width, were obtained from the recent Zanzibar and Pemba collections (2000, 2009) housed in the Department of Natural

Sciences, National Museum of Wales (Ben Rowson, pers. comm., 29 November 2014). The independent control sample structure and descriptive statistics are presented in Table 2.

The data were log-transformed (base-10) as this process tends to make the data linear, normally distributed and homoscedastic, allowing for linear regression (ordinary least squares) techniques to be applied (Campbell 2008, 2013). The linear regression equation for log-transformed data using this method is: $\log(y) = \log(A) + b \log(x)$. Each log-transformed measurement variable was plotted against log shell length, with no clear outliers influencing the observations. The results of the correlation, linear regression and significance tests for the log-transformed data are presented in Table 3. In all cases, the correlation coefficients (r and P values) indicate a strong positive and significant linear correlation between shell length and each measurement. The coefficients of determination obtained for each variable (r^2) are also very high (all ≥ 0.960). The addition of more specimens per taxon across the growth range would likely strengthen the predictive power, in addition to testing the validity of the equations on an independent sample (Campbell 2013:8), however for the purposes of this exploratory analysis each log-transformed measurement variable is viewed here as being a useful predictor of shell length for all three *Achatina* species. The log-based prediction equation and coefficients of determination require transformation to estimate shell length in the original scale (mm). The following antilog equation is used in each instance: $y = 10^a (x^b)$, incorporating the coefficients of determination presented in Table 3.

Results

Kuumbi Cave Assemblage Characteristics

Due to the differential preservation of diagnostic features for identification, the material recovered from Kuumbi Cave has been attributed to a large number of taxonomic categories (Table S1), increasing in quantity from the lowest contexts into context 1018, where the number of categories fluctuates at a comparatively higher level before decreasing significantly into the upper context 1000.

A total of 80 invertebrate taxonomic categories have been recorded, with 35 to species level (nine terrestrial gastropods, two marine bivalves and 24 marine gastropods), 23 to genus level (one terrestrial gastropod, four marine bivalves and 19 marine gastropods) and 17 to family or subfamily level (seven marine bivalves and 10 marine gastropods). The Decapoda (crab), Cirripedia (barnacle), Polyplacophora (chiton) and Echinoidea (urchin) have been recorded to class or infraclass level. Juvenile specimens (*Achatina* spp. and *Atactodea* sp.) have been listed and quantified separately in Table S1 but are not included in the above overview as distinct taxonomic categories.

The overall condition of the marine shell is characterised by a low to moderate degree of fragmentation, with low to moderate levels of dissolution and chemical degradation. No specimens were recorded with evidence of beachrolling, boring or epibiont adhesions. In contrast, the Achatinidae demonstrated a moderate to high degree of burning throughout the KC10 sequence with a high degree of fragmentation (only 18 complete specimens in total for the entire deposit). No specimens/fragments exhibited evidence of non-human predation in comparison with the modern Jozani samples, some of which showed evidence of rodent biting, crab peeling or body whorl damage more characteristic of mongoose behaviour (Kasigwa et al 1983). Additionally, no specimens retained evidence of human modification linked to the use of *Achatina* spp. shell as implements or for ornamental use, as discussed recently by Walz (2016, 2017) for lowland northeastern Tanzania.

The total assemblage is represented by an MNI of 3151 (recalculated relative to the 3556 MNI presented in Shipton et al. 2016:210; Prendergast et al. 2016), presenting a multi-modal distribution through the Kuumbi Cave sequence (Figure 4A), gradually increasing into context 1018 (Phase 3, Late Pleistocene), followed by fluctuating abundances with peaks in the distribution in contexts 1017 (Phase 2, terminal Pleistocene), 1011, 1007 and 1004 (Phase 1, MIA-LIA). Separating the assemblage into marine and terrestrial taxa, there is a total marine MNI of 2129 (68%) and total terrestrial MNI of 1018 (32%), with relative abundance by context showing a differential distribution through the sequence (Figure 4B and C). The Decapoda (MNI = 4) have been excluded here; the degree of fragmentation and lack of preserved diagnostic features means that the crab remains are unable to

be assigned to a more accurate taxonomic category, and as such the likely habitat (terrestrial vs marine) and origin (e.g. natural vs. cultural) are ambiguous. As noted above, there were different sampling and recovery methods used between the broad marine and terrestrial molluscan categories, therefore the volume corrected (MNI/m^3) distributions provide a more useful comparison. Terrestrial taxa density peaks in the late Pleistocene (contexts 1019 and 1022 in Phase 3) and again in the MIA-LIA (context 1005 in Phase 1), and while the density distribution varies throughout the rest of the deposit, the terrestrial molluscs occur at relatively higher densities than marine species. The dense escargotière, or land snail midden layer, in context 1019 is shown in Figure 4D, and the significance of this context in the Kuumbi Cave sequence is highlighted in Figure 4E, where the density of land snail (MNI/m^3) is compared for the major contexts only (removing the minor contexts 1005, 1016, 1020, 1022 and 1023). Occurring at low levels throughout the bottom four contexts, marine taxa peak within contexts 1022 (Phase 3), 1016 (Phase 2) and 1005 (Phase 1), again demonstrating a variable density throughout the rest of the sequence and decreasing into the upper-most contexts of the MIA-LIA. Even given the differences in the major peaks between the marine and terrestrial invertebrates within the late Pleistocene Phase 3, there are some broad similarities in these distributional patterns, both demonstrate a reduction in density within the upper contexts of Phase 2 (terminal Pleistocene-early Holocene transition) to then increase through the lower contexts of the MIA-LIA Phase 1. There is also a substantial decrease in density for both broad classes in context 1004, and again in 1000.

Within these figures there are several taxa that likely represent natural incorporations into the deposit, including the terrestrial gastropods *Maizania zanzabarica*, *Tropidophora zanguebarica*, *Edentulina obesa*, *Edentulina ovoidea*, *Homorus* (*Subulona*) *usagarica* and *Pseudoglessula subolivacea* agg., in addition to the juvenile Achatinidae. Other taxa that likely represent incidental collection (i.e. as potential by-products of foraging rather than for economic or subsistence purposes) are the juvenile *Atactodea* sp., Fissurellidae and *Hipponix* spp. Exclusion of these taxa or categories, in addition to the Decapoda noted above, do not change the broad trends highlighted here given their

low abundance, with only nine individuals (0.3%) represented within the marine taxa and 58 individuals (1.8%) from the terrestrial taxa.

The Dominant Economic Taxa

Excluding the incidental categories to focus on the potentially economic species (representing 71 taxonomic categories at 3084 MNI), the dominant taxa are *Nerita balteata* (429 MNI, 13.9%), *Achatina reticulata* (411 MNI, 13.3%), *Turbo setosus* (306 MNI, 9.9%), *Nerita plicata* (250 MNI, 8.1%), *Achatina* spp. (245 MNI, 7.9%), *Nerita textilis* (201 MNI, 6.5%), *Achatina fulica* (171 MNI, 5.5%), *Nerita albicilla* (169 MNI, 5.5%), *Achatina allisa* (133 MNI, 4.3%), Polyplacophora (130 MNI, 4.2%), *Lunella coronata* (123 MNI, 4.0%) and *Nerita polita* (115 MNI, 3.7%). Together these taxa comprise 87% of the total economic species within the Kuumbi Cave assemblage, and except for the Polyplacophora, can be combined to three main taxonomic categories at family or genus level (*Achatina* spp., *Nerita* spp. and Turbinidae). The distribution of these combined taxonomic categories by context (MNI and MNI/m^3) is presented in Figure 5. The *Nerita* spp. and Turbinidae demonstrate similar patterns in distribution, albeit with the Turbinidae at lower densities through the sequence. Both taxa peak in contexts 1022, 1020 (Phase 3) and 1016 (Phase 2), with the *Nerita* spp. also increasing in density in context 1005 (Phase 1). The *Nerita* spp. were not identifiable in the putatively non-cultural Phase 4 (contexts 1025 and 1026), with the Turbinidae only represented by a single individual in the pre-20 ka context 1025, and both decrease into the upper Phase 1 LIA (1000). The *Achatina* spp. show a different distributional pattern, with higher densities through most of the deposit, peaking in contexts 1019 and 1022 (Phase 3) and again in 1005 (Phase 1), and disappearing entirely in context 1000.

Viewing the density and distribution patterns for the Achatinidae species level attributions demonstrates relatively similar trends through the Kuumbi Cave sequence for *A. reticulata* (Figure 6A), *A. fulica* (Figure 6B) and *A. allisa* (Figure 6C). *A. reticulata* dominates the land snail assemblage, mainly in the late Pleistocene contexts within Phases 2 to 4, with particularly pronounced peaks in the

distribution in Phase 3 contexts 1019 and 1022 corresponding with the dense escargotière layers (in combination with *A. allisa*). This taxon also presents a relatively consistent density through the late Holocene MIA-LIA Phase 1 contexts (excepting 1003 and 1000). *A. allisa* and *A. fulica*, while broadly conforming to the same trends as *A. reticulata*, exhibit slight differences in their distribution. *A. allisa* is more abundant in the lower contexts of Phase 3 (1024 and 1019) and in Phase 1 context 1005, whereas *A. fulica* peaks in the upper part of Phase 3 (context 1022) and displays a higher density in the upper part of Phase 1 (like *A. reticulata*). These distribution and density patterns suggest differential exploitation, related potentially to pulses in natural mollusc population expansion, phases of human occupation of the site, and/or habitat structure and resource availability within and between each chronological phase at Kuumbi Cave.

Habitat Representation

An analysis of relative abundance per habitat category for the total economic and non-economic taxa at Kuumbi Cave (by %MNI and %MNI/m^3) indicate an overall focus on three main habitat categories: woodland/forest litter, intertidal or shallow subtidal reef/rock, and supratidal rock/mangrove (Figure 7). These three habitats zones account for 93% of MNI (99% MNI/m^3) across all phases, with these trends holding when the economic and non-economic taxa are examined separately and combined. Broadly, these data demonstrate a decline in terrestrial, forest dwelling taxa (*Achatina* spp.) with a concurrent increase in supratidal mangroves and rocks (primarily *Nerita* spp. and Polyplacophora), and intertidal and shallow subtidal reefs and rocks (primarily Turbinidae and Cypraeidae). All other habitat categories represent very minor components of the assemblage, with only intertidal or shallow subtidal sand/mud contributing greater than 10% of MNI overall, for a total of 12.3% MNI (136 MNI) across all phases. The preliminary analyses presented by Shipton et al. (2016:224) for minimal shifts in molluscan habitat representation holds at a relatively coarse analytical level, however greater variability in taxonomic exploitation and habitat representation becomes apparent with increased

analytical resolution. A chi-squared test indicated a significant association between phase and habitat category (MNI) (X^2 [20, n = 3151] = 286.07, p = < 0.001, Monte-Carlo p = 0.0001, V = 0.213) that holds for volume corrected samples. Cramer's V demonstrated that the effect size was small to medium (Cohen 1988). Examination of adjusted residuals (Table 5) showed that there was significantly greater MNI from woodland/forest litter habitats in the late Pleistocene Phase 3/4, significantly more individuals from intertidal or shallow subtidal reef/rock in the terminal Pleistocene Phase 2, and significantly greater MNI from intertidal or shallow subtidal sand/mud and supratidal rock/mangrove habitats in the MIA-LIA Phase 1. These trends hold for both raw and volume corrected abundance estimates by context (Figure 7). Terrestrial, forest dwelling taxa (*Achatina* spp.) peak in relative abundance in Pleistocene deposits, accounting for between 64-97 %MNI/m^3 in the Phase 3 and 4 contexts. Within the middle portion of the deposit, taxa from terrestrial habitats decline rapidly, accounting for between 6.2-18% MNI/m^3 in contexts 1020-1011. At the same time, the relative abundance of intertidal or shallow subtidal reef/rock (primarily *Nerita* spp. and Turbinidae) and supratidal rock/mangrove taxa increases, with a later (contexts 1000-1011) shift away from intertidal or shallow subtidal reef/rock toward an increased reliance on supratidal mangroves.

Richness, Diversity and Variability in Economic Taxa Representation

Nestedness analyses, following combination of each taxonomic category to the highest common level, indicate highly nested assemblages for Phase 1 (Figure 8A), Phase 2 (Figure 8B) and combined Phases 3 and 4 (due to low Phase 4 sample sizes; Figure 8C), with low temperatures (7.95°-23.17°) indicating that each sample has been drawn from the same source population. In fact, the total site assemblage indicates a high degree of nestedness (T = 17.62°) regardless of chronological phasing. Inspection of the species area curves (Figures 8A, B and C) also indicates sampling to redundancy for each phase.

Similar to the recent analyses undertaken by Otaola et al. (2015) and Wolverton et al. (2015) on Argentinian assemblages, taxonomic richness, diversity and proportional abundance of key species

(Table 6) are analysed here to discern diachronic trends in mollusc foraging at Kuumbi Cave. Temporal trends in NTAXA (Figure 9A) indicate increasing richness through the sequence into context 1015 (upper Phase 2 terminal Pleistocene), followed by higher levels of variability through the Phase 1 MIA-LIA contexts (although still demonstrating a general increasing trend to peak in context 1003), with a considerable decrease into recent the LIA (context 1000). This chronological trend is more apparent by Phase, where median richness values increases from Phase 3/4 (NTAXA = 6), to Phase 2 (NTAXA = 12) and Phase 1 (NTAXA = 13.5). In evaluating assemblage heterogeneity, the trends in the Shannon Index (*H*) and Simpson's Index (1-*D*) through the Kuumbi Cave sequence demonstrate some important differences relative to richness. Both the Shannon and Simpson's (Figure 9B) indices for the total assemblage show an increase in diversity from the lowest four contexts of Phase 3/4 (1019, 1024, 1025 and 1026), with very low diversity values reflecting a clear separation from Phases 1, 2 and the upper contexts of Phase 3 due to the dominance of the Achatinidae within these lowest contexts. Diversity peaks in contexts 1020 (upper Phase 3) and 1016 (mid Phase 2) for the Shannon and Simpson's Indices respectively, with a subsequent decline through the upper contexts, although both measures show a slight reduction at the start of Phase 1 followed by an increase prior to dropping into the upper contexts. Median diversity values increase from Phase 3/4 (*H* = 1.04; 1-*D* = 0.51), to Phase 2 (*H* = 1.64; 1-*D* = 0.73) and with a slight decline into Phase 1 (*H* = 1.43; 1-*D* = 0.66), demonstrating the pattern of diversity increasing into the terminal Pleistocene with a subsequent decrease in the late Holocene.

Calculating the Shannon (*H*) and Simpson's (1-*D*) indices for the marine taxa only (Table 6, Figure 9C) provides relatively subtle differences in diversity, yet still highlights the effect the Achatinidae have on Kuumbi Cave assemblage structure. Both indices present their lowest values in context 1019 (late Pleistocene) and peak in context 1005 (MIA-LIA), and although variable in distribution across contexts within each phase, the overall trend in marine diversity is one of relative consistency. This is emphasised by the median diversity values by phase, with the Shannon index exhibiting only a minor increase in diversity in the terminal Pleistocene Phase 2 contexts (Phase 1 = 1.35; Phase 2 = 1.45; Phase

3 = 1.39), and Simpson's index exhibiting a slight decrease in the late Holocene (Phase 1 = 0.60; Phase 2 = 0.66; Phase 3 = 0.67).

The land snail index (Figure 10A) demonstrates a decreasing trend through the late Pleistocene contexts of Phase 3/4 and into the terminal Pleistocene-early Holocene transition of Phase 2, reflecting the increasing prevalence of the dominant marine mollusc taxa through time. In comparison, the land snail index through Phase 1 shows a higher level of variability, with a slight increase in the trend toward the latter part of the sequence. Median land snail index values decrease from 0.61 in Phase 3/4 to 0.20 and 0.39 in Phase 2 and 1 respectively. As this index is based on the MNI counts rather than volume corrected estimates, this likely underestimates the relative importance of the Achatinidae, however it does demonstrate the increasing prevalence of marine invertebrates, with median volume-corrected land snail index values decreasing from 0.80 in Phase 3/4 to 0.62 and 0.63 in Phases 2 and 1. The combined *Nerita* spp. index decreases through the Pleistocene Phase 3/4 and 2 contexts (Figure 10B), exhibiting slightly higher values at the start of Phase 1 to decrease into the more recent LIA contexts. Even given this degree of variability, when excluding context 1025 in Phase 4, the *Nerita* spp. demonstrate a consistently high proportional abundance as small bodied marine taxon relative to the larger Turbinidae. This is emphasised by the median *Nerita* spp. index values by phase, which show a slight decrease from Phase 3/4 (0.68) into Phase 2 (0.64), increasing again into Phase 1 (0.77). Finally, the *Achatina reticulata* index (Figure 10C) is high through the Phase 3/4 contexts, more variable in Phase 2 given the lower value in context 1015, and decreasing throughout the MIA-LIA (Phase 1). Overall there is a decreasing trend in proportional abundance of the large *A. reticulata* relative to the medium sized *A. fulica*. Again, the phase median values highlight this trend, with *A. reticulata* decreasing from Phase 3/4 (0.79) into Phase 2 (0.64) and Phase 1 (0.62).

Achatina *spp. Size Analyses*

As a means of exploring the size range of the Achatinidae recovered from Kuumbi Cave, and potential size selectivity in their exploitation, shell lengths for each of the three Achatina species were reconstructed using the morphometric equations established above. None of those specimens designated to genus level were included in the sample, being largely composed of non-diagnostic spire fragments. Descriptive statistics for the predicted shell lengths for the total sample and by Phase for each species are detailed in Table 7, with the total sample size frequency distributions for predicted shell length presented in Figure 11.

The *A. allisa* predicted shell length statistics and size frequency distributions (Figure 11A) for the total sample (n=15; 11.3% total taxon MNI) indicate a median predicted shell length of 61.54 mm, with size ranging between 41.57 and 77.99 mm. This distribution is bimodal, with low negative skew (-0.40) and low positive kurtosis (0.19), indicating a near normal, symmetrical mesokurtic distribution. The *A. fulica* total sample (n=40; 23.4% total taxon MNI) statistics indicate a median predicted shell length of 57.78mm, with size ranging between 44.09 and 98.85 mm. The assemblage is bimodal in its distribution (Figure 11B) and is also highly positively skewed (2.10) with a high positive kurtosis (4.90) value, indicating an asymmetrical leptokurtic distribution with a long tail extending into the larger size classes. For *A. reticulata* (n=126; 30.7% total taxon MNI), there is a total sample median predicted shell length of 150.10mm and size range between 65.73 and 218.58 mm. This sample demonstrates a multimodal distribution (Figure 11C), moderate negative skew (-0.58) and low negative kurtosis (-0.05), showing an almost symmetrical mesokurtic distribution in comparison with that illustrated for *A. fulica*. Although these data are based on very small sample sizes and are highly time-averaged, it is possible that the bimodal or multimodal distributions may in part represent different seasonal recruitment periods. Regardless, given the relatively restricted size distributions and overall high density of each taxon, it is tentatively suggested due to the limited sample sizes that these data reflect a high degree of size selectivity linked to human exploitation.

Comparing predicted shell size by phase, *A. allisa* (Figure 12A) demonstrates a decrease in mean and median values as measures of central tendency, and a slight decrease in the size ranges through time

between the late Pleistocene (Phase 3) and the MIA-LIA (Phase 1). A Mann-Whitney U test (*Mdn* = 61.54, *U* = 38.0, *z* = 1.157, *p* = 0.281, *r* = 0.29), however, indicates that these observed differences are not significant. For *A. fulica* (Figure 12B) there is a degree of variability in both mean and median values across Phases 1, 2 and 3, with a more restricted size range occurring in the terminal Pleistocene Phase 2 compared with Phases 1 and 3. A Kruskal-Wallis test (*H* (2) = 0.227, *p* = 0.893, η^2 = 0.01) confirms that the trends observed in the central tendency across these three phases are not significant. A similar pattern occurs with the *A. reticulata* samples, where there is again a degree of variability in mean and median values, as well as overall size ranges, across all four Phases (Figure 12C). There is an apparent decrease in shell size through the sequence, however Kruskal-Wallis test results (*H* (3) = 6.759, *p* = 0.080, η^2 = 0.05) again confirm that this is not significant. These results are cautiously attributed again to foraging size selectivity, suggesting that people were consistently exploiting those larger individuals available from within Kuumbi Cave and the surrounding environment.

Discussion/Conclusion

A Review of Mollusc Exploitation at Kuumbi Cave

The data presented in the analyses above are significant for several reasons. Firstly, the number of taxa has been expanded considerably compared to the preliminary report in Shipton et al. (2016), highlighting the degree of invertebrate assemblage richness, and providing a baseline from which to investigate diversity and the nature of mollusc exploitation at a higher degree of resolution. Secondly, these data show that marine invertebrate exploitation occurred much earlier at Kuumbi Cave than previously recognised (Chami 2009; Sinclair 2007; Sinclair et al. 2006), with clear evidence for use of these resources during the Pleistocene rather than being initiated in the mid Holocene. Supported by the range of analyses and indices outlined above, together these data suggest a longer-term trajectory in coastal resource exploitation and coastal economic adaptations in the region, beginning potentially

by at least c. 18 ka, and definitely by c. 13 ka. In addition to the marine component, Kuumbi Cave is important as it one of the few sites in eastern Africa that shows significant levels of exploitation of large terrestrial gastropods.

What the data also indicate within these long-term trends, however, is variability rather than consistency in foraging activity. This trend is mostly likely linked to environmental variability and resource/habitat structure within the punctuated or episodic pattern of occupation at the site. While there was an emphasis on the terrestrial *Achatina* spp. through the sequence to the late Holocene (MIA-LIA), the peaks and troughs in the density and distribution of these taxa would suggest differential exploitation through time to a degree. It is likely that this represents human exploitation whereby people were taking advantage of natural pulses in Achatinidae population increase in forested environments around Kuumbi and/or aestivating populations within the cave. While there was a primary emphasis on the larger *A. reticulata*, the data suggests differential exploitation of the medium to small-bodied *A. fulica* and *A. allisa* depending on their availability and density. The proposed initial phase of occupation (or at least intensive occupation) at the site, in the late Pleistocene c. 19-17 ka (contexts 1024 and 1019), is dominated by terrestrial specimens with relatively few marine individuals per m^3. Following the initial economic emphasis on terrestrial species exploitation, relatively more marine individuals were exploited from context 1018 (Phase 3) and again in Phase 2 (13-11 ka).

The terminal Pleistocene-early Holocene period represented within Phase 2 would have been marked by rapid sea level rise and environmental/habitat reconfiguration. Habitat representation at the site can be broadly categorised, therefore, as showing an early focus on terrestrial taxa in the Pleistocene, with correspondingly low assemblage richness and low dominance values (particularly in the late Pleistocene assemblages of Phase 4 and the lower units of Phase 3). At the same time, there is an increase in both total mollusc assemblage richness and the relative abundance of intertidal or shallow subtidal reef/rock and supratidal rock/mangrove taxa, possibly indicating expanding marine diet breadth correlated with a more intensive focus on newly developed intertidal habitats following sea-

level rise. Later, LIA-MIA deposits indicate a shift away from intertidal/shallow subtidal reef/rock, with a richer and less diverse assemblage demonstrating another shift in habitat selection to focus less intensively on intertidal habitats, and toward a foraging strategy that sees increased (albeit punctuated) reliance on terrestrial taxa and molluscs from the now well-established supratidal mangroves.

When considering the different patterns evident between the terrestrial and marine taxa through time at Kuumbi Cave, a significant degree of foraging strategy switching becomes apparent. There was a higher degree of selectivity in the exploitation of the Achatinidae through time, illustrated by the proportional abundance of the three taxa and size analyses. There was not, however, a sole focus on *A. reticulata* as the largest taxon. There appears to have been a degree of switching between taxonomic size classes, particularly during the terminal Pleistocene and the late Holocene (Phases 2 and 1), which would more likely reflect differential availability and potentially seasonality in exploitation, rather than a decrease in foraging efficiency or resource depression of a larger-bodied invertebrate resource. The structure and composition of the marine assemblage is generally linked to habitat availability, with a principal focus on foraging within certain locations within the intertidal and near-shore zone, and changes through time linked to post-glacial sea level rise and variability. This still represents a certain degree of patch or habitat choice, even if these were the dominant coastal habitat zones within a given time period, with selectivity potentially linked to a range of other logistical economic activities for exploiting certain near shore zones (such as fishing). Within the dominant habitat, it is possible that exploitation of the range of taxa represented within the Kuumbi Cave marine mollusc assemblage represents their naturally occurring abundance and availability, following an indiscriminate foraging strategy akin to habitat sweeping (e.g. Faulkner et al. 2017; Harris and Weisler 2017:19; Szabó 2009:208; Szabó and Amesbury 2011). That said, it is somewhat difficult to assess the nature of the foraging strategy used for the exploitation of marine molluscs in this instance, due to potential issues of differential processing and transportation between 2.5 and 8 km inland from the coast to Kuumbi Cave (Bird and Bliege Bird 1997; Bird et al. 2002; Giovas 2016). The differential

dominance of the Neritidae and Turbinidae within the assemblage may also therefore relate to the transportability of these taxa (e.g. Manne and Veth 2015), rather than a simple direct reflection of the full marine diet breadth. This is particularly the case given the degree of socio-economic restructuring and variability in settlement and mobility known for the MIA-LIA in eastern Africa (e.g. Fleisher et al. 2015) but may also be a factor within and between the earlier phases of occupation within Kuumbi Cave.

The Kuumbi Cave Vertebrate Fauna: A Brief Comparison

Understanding the economic role of invertebrate resources requires positioning these data within the broader faunal trends through the Kuumbi Cave sequence. Here we briefly consider the main trends in the fish and tetrapod assemblages within which to position the discussion of the molluscan material. This last point links strongly to the structure of the tetrapod assemblage through time. Within Phase 4 a diverse range of terrestrial mammals are present (represented by 152 NISP), including small and large bovids, zebra, monkey and hyrax (Shipton et al. 2016:213). In Phase 3 (2867 NISP) and Phase 2 (1179 NISP), the assemblage is largely comprised of duikers and suni (small bovids), although the overall range of taxa suggests a broad subsistence base, including bushpig, reedbuck, bushbuck, waterbuck, buffalo and zebra as the larger-bodied animals occurring in low numbers (Prendergast et al. 2016; Shipton et al. 2016:215-6). Finally, in the late Holocene Phase 1 (2469 NISP), the range of fauna remains relatively consistent with that seen in the Pleistocene contexts, being dominated by small bovids and other small-bodied fauna. The pattern across the four phases indicates a high degree of consistency in the exploitation of the dominant tetrapod taxa through time. However, by the late Holocene occupation phase, there are several faunal extirpations (Prendergast et al. 2016; Shipton et al. 2016:223), including zebra, buffalo, waterbuck, reedbuck and bushbuck, as well as the smaller steenbok and bush duiker. Prendergast et al. (2016) have identified the persistence of certain smaller-bodied taxa within a trend of decreasing abundance of large and medium-sized taxa through time

(potentially linked to an anthropogenic cause), in combination with tetrapod assemblage richness decreasing over the course of the late Holocene.

Marine fish within late Pleistocene contexts at Kuumbi Cave (Phase 3), represent the earliest known evidence for maritime fishing in eastern Africa (Shipton et al. 2016:216). Although the small sample size (NISP=11) is interpreted as indicating that fishing was not a significant economic activity at the time (although again this may be linked to distance from the coast and transportation of these resources), the taxa represented occur in nearshore habitats, and correlate with the increase in marine molluscs deposited within Phase 3. Between the late and terminal Pleistocene (phases 3 and 2) and MIA-LIA (Phase 1), the fish sample size increases (90 NISP), with the dominant taxa (parrotfish, Scarinae) coming from reef habitats (Shipton et al. 2016:223). This supports to some degree the original suggestion by Prendergast et al. (2016) for a broadening of the diet, inclusive of marine molluscs and fish, as larger-bodied terrestrial faunal resources begin to be depleted by the terminal Pleistocene/early Holocene. This interpretation is complicated when the invertebrate assemblages are considered in greater detail, particularly by the points highlighted above regarding differential exploitation and transportation of coastal resources, the possibility of several phases of economic re-organisation, particularly when Kuumbi Cave was not occupied, and the lack of other comparative sites or datasets from the region falling within the same time periods (the latter also noted by Prendergast et al. 2016). Taken together, these data are at least suggestive of increasing marine diet breadth and coastal resource use within the earliest periods of occupation at the site.

Summary and Implications

In contextualising the archaeomalacological data with the vertebrate faunal assemblages recovered from Kuumbi Cave, several implications for our understanding of the economic structures represented within the sequence become apparent. Occupation at Kuumbi Cave increased in intensity c. 19-17 ka (with earlier, less intensive occupation older than c. 20 ka in Phase 4 possible), with the late

Pleistocene economy representing significant diet breadth, encompassing a range of small, medium and large terrestrial vertebrates, small numbers of marine fish and molluscs, and significant numbers of large terrestrial molluscs. In many respects, the terminal Pleistocene (c. 13-11 ka) contexts of Phase 2 demonstrate a relatively similar economic structure, albeit with a reduction in the proportional abundance of large to medium tetrapods and the Achatinidae, with a concomitant proportional increase in marine molluscs. As noted above, the trend towards higher marine invertebrate deposition at Kuumbi Cave likely relates to decreasing distance from the coast (following the LGM with sea level rise) combined with coastal habitat development and modification. While the late Pleistocene and terminal Pleistocene phases of occupation both reflect generalised foraging strategies, the subtle differences in economic structure between these periods are suggestive of shifts in the use of the broader landscape and potentially the differential abundance of resources available in the forests around Kuumbi Cave and on the adjacent coast.

The degree of consistency in small to medium tetrapod exploitation within each of the earlier three phases of occupation provides an interesting context for the exploitation of the Achatinidae. Given the relative dominance of the molluscan assemblage across each Phase of the Kuumbi Cave sequence, the large land snails can be seen to be one of a number of components of a broad-based foraging strategy, with people actively exploiting the full range of resources available to them from the forested environments surrounding the site. The Achatinidae thus appear to have been an easy to access resource for human populations during the initial phase of occupation at Kuumbi Cave before stabilising as one component of a broader diet during the terminal Pleistocene.

Assessing the way in which the MIA-LIA assemblage recovered from Kuumbi Cave connects more broadly to the socio-economic structures of this late Holocene period (for details see Crowther et al. 2017; Fleisher et al. 2015), particularly following a significant hiatus period from the terminal Pleistocene, is potentially more complex. This is particularly the case prior to the development of the denser urban settlements of the LIA, where the zooarchaeological data from several MIA sites (notable Unguja Ukuu and Fukuchani on the west and northwest coast of Zanzibar) indicates a mixed economy

of fishing, hunting/trapping and foraging as important components alongside herding and farming (Faulkner et al. 2018; Prendergast et al. 2017:635). The emerging pattern of Swahili subsistence economies on the coast is one of diversity, incorporating a significant degree of hunting and foraging alongside food production (e.g. Crowther et al. 2017; Faulkner et al. 2018; Prendergast et al. 2017; Quintana Morales and Horton 2014).

It has been suggested that the late Holocene occupants of Kuumbi Cave, particularly in the MIA (contexts 1011-1003), may have been full-time foragers who had contact with food producers on the coast (Crowther et al. 2017:12), with several important lines of evidence supporting this interpretation. The MIA contexts contain distinctive early Tana Tradition/Triangular Incised Ware (TT/TIW) ceramics, like those seen at Unguja Ukuu and Fukuchani, but representing a local variant due to differences in fabric and decoration (Shipton et al. 2016:220-221). Drawing on ethnographic data relating to forager and food producer hunting preferences (following Prendergast and Mutundu 2009), in addition to detailed analyses of the Kuumbi Cave vertebrate faunal assemblage indicating high diversity of wild taxa and more expansive exploitation of near-shore fish, Prendergast et al. (2016) also suggests hunter-gatherer occupation at Kuumbi Cave during the MIA. Finally, recent ancient DNA evidence from human remains recovered from Context 1011 and directly dated to 1370-1303 cal BP (c. 600 CE) indicates greater affinity and ancestral connections with the Khoe-San of southern Africa than with present-day Bantu speakers in eastern Africa (Skoglund et al. 2017:62). Based on this evidence there appears to have been initial genetic isolation between early Bantu speaking farmers (such as those at Unguja Ukuu) and established foraging groups during the MIA Africa (Crowther et al. 2017; Skoglund et al. 2017:63-64).

In this context, the decreasing tetrapod richness, large to medium faunal extirpations, and the increasing abundance of marine fish reflects a late Holocene expansion in diet breadth (and therefore an important phase of economic reorganisation), and interpretation that is well supported by the archaeomalacological data. In the MIA-LIA the data indicates persistence of molluscan taxa from reef/rock environments, and in addition to the increasing prevalence of upper littoral mangrove taxa

in the more recent deposits, this would imply a possible shift in logistical foraging and/or access to a range of near shore marine resources, and potentially differential transportation of subsistence remains from the coast to Kuumbi Cave.

Conclusion

As small-bodied resources, particularly when compared with terrestrial and marine vertebrate species, molluscs have often been assumed to fill an economic role as secondary or supplementary resources (see discussions in Braje et al. 2011 and Erlandson 1988, 2001). While this is undoubtedly the case in certain contexts through time and space (e.g. Bailey 1975; Kuhn et al. 2009), there are also instances where they are significant dietary components in palaeoeconomic structures, forming one of a number of components of a broad-based foraging strategy (e.g. Bicho and Haws 2008; Colonese et al. 2011; Erlandson 2001; Jerardino 2010) or even constituting one of the principal resources supporting past populations (e.g. Braje et al. 2011; Faulkner 2013; Erlandson et al. 2004; Ono et al. 2010). At Kuumbi Cave, invertebrates do not appear to fall neatly into a single category whereby they can be easily defined as secondary or supplementary resources. For the total spectrum of invertebrate taxa recovered from Kuumbi Cave, both the terrestrial and marine molluscs, their importance lies in their relative reliability as a protein source along with their support of other nutritional requirements (e.g. Erlandson 1988; Kyriacou et al. 2015; Meehan 1982), combined with there being comparatively less risk in their procurement compared to other protein sources, together with the fact that they can be mass harvested (Braje and Erlandson 2009; Faulkner et al. 2017; Perlman 1980).

Based on the detailed analyses of the dense Achatinidae deposits within the site presented above, these taxa would appear to be important components of a broad-based foraging strategy, and a key, easy-to-access resource for people during initial occupation of the site. A broad-based foraging strategy is particularly evident when the terrestrial molluscs are contextualised within the broader vertebrate faunal evidence linked to general forest environment exploitation. This is also the case for

the increasing prevalence of marine mollusc taxa from c. 18 ka, continuing into the terminal Pleistocene phase, and again during the late Holocene MIA-LIA deposits. This suggests an early engagement with near-shore resources, and certainly highlights coastal resource use well before the onset of post-glacial sea level rise in the region.

The notion that marine invertebrates were considered lower-ranked resources is not supported by the Kuumbi Cave data. Although occurring variably through the deposit in terms of taxonomic composition, as a resource category they were exploited at relatively consistent levels throughout the sequence of occupation (apart from during the LIA, likely linked to shifts in socio-economic and settlement structures during the Swahili period). Marine species would have required transportation up to 8 km inland, particularly during the late Pleistocene phases of occupation. Given the possibility for multiple phases of socio-economic reorganisation through time (sensu Prendergast et al. 2016), and multiple reorientations of logistical resource acquisition and mobility between Kuumbi Cave and the coast, these data may speak to a long-term trajectory in coastal adaptations (as a transformative and non-linear process affecting economic, mobility and settlement structures) rather than simply coastal resource use, whereby marine resources are used systematically but where lifeways are not significantly altered (see for example discussions in Beaton 1995; Crowther et al. 2016; Fleisher et al. 2015; Marean 2014). While more data are needed to effectively test the relationship between people, near-shore resources, and the possibility of the intensification of marine exploitation through time, the evidence from Kuumbi Cave suggests that marine molluscs were more than simply a dietary supplement in prehistoric coastal eastern Africa.

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Figures

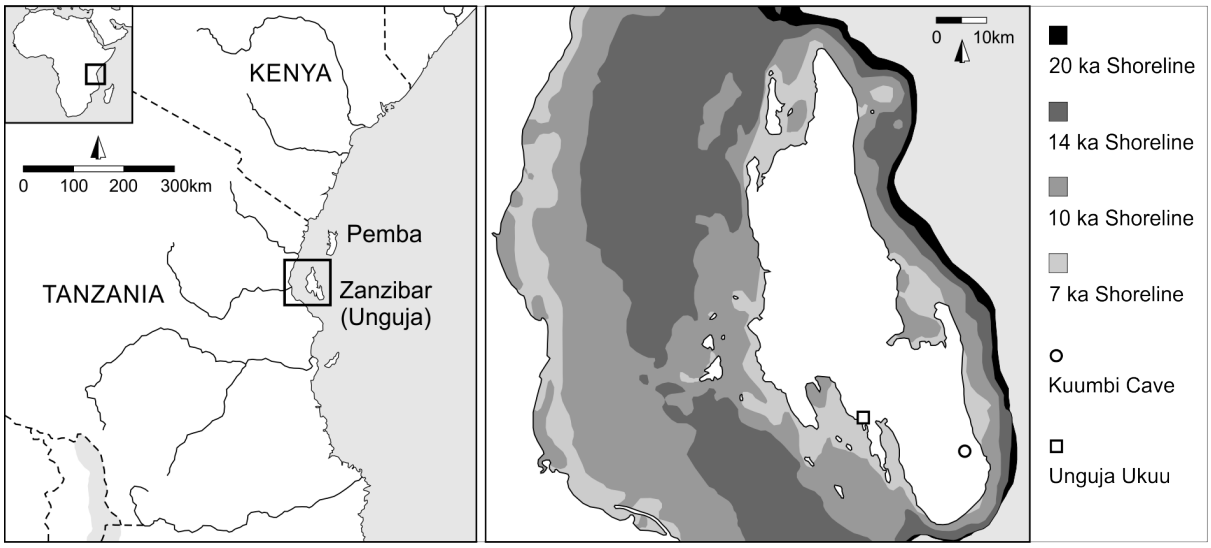


Figure 1: Location of Kuumbi Cave and relative shoreline position 20 ka to present

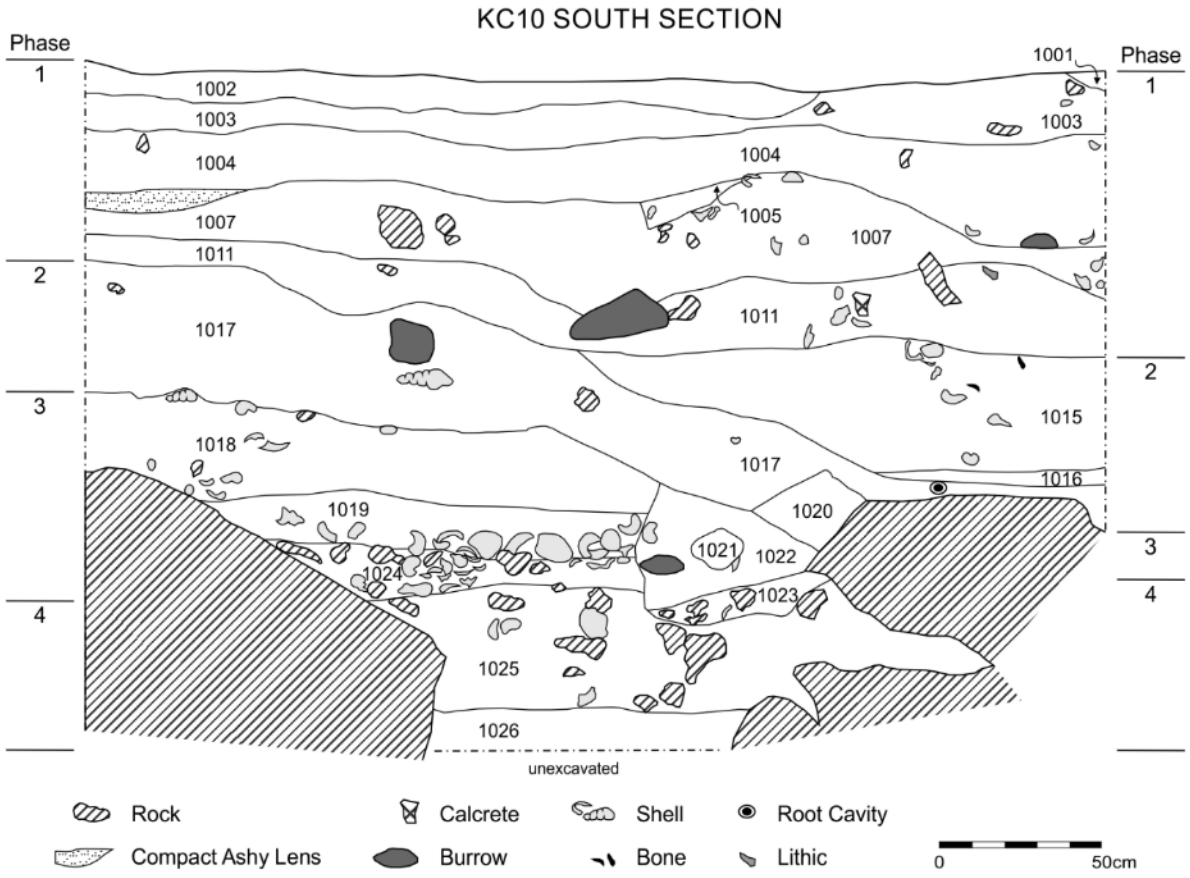


Figure 2: Kuumbi Cave Trench 10 South stratigraphic section (redrawn from Shipton et al. 2016), showing context and phase groupings

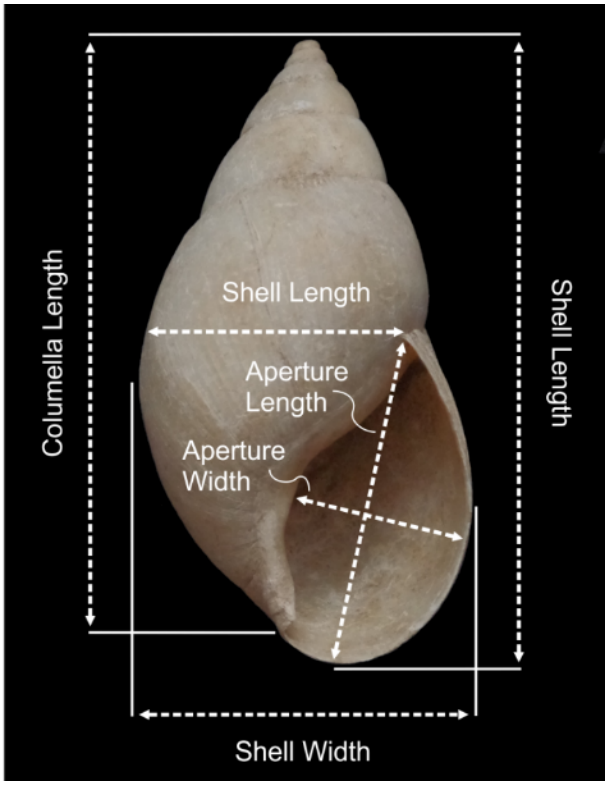


Figure 3: *Achatina* species measured attributes

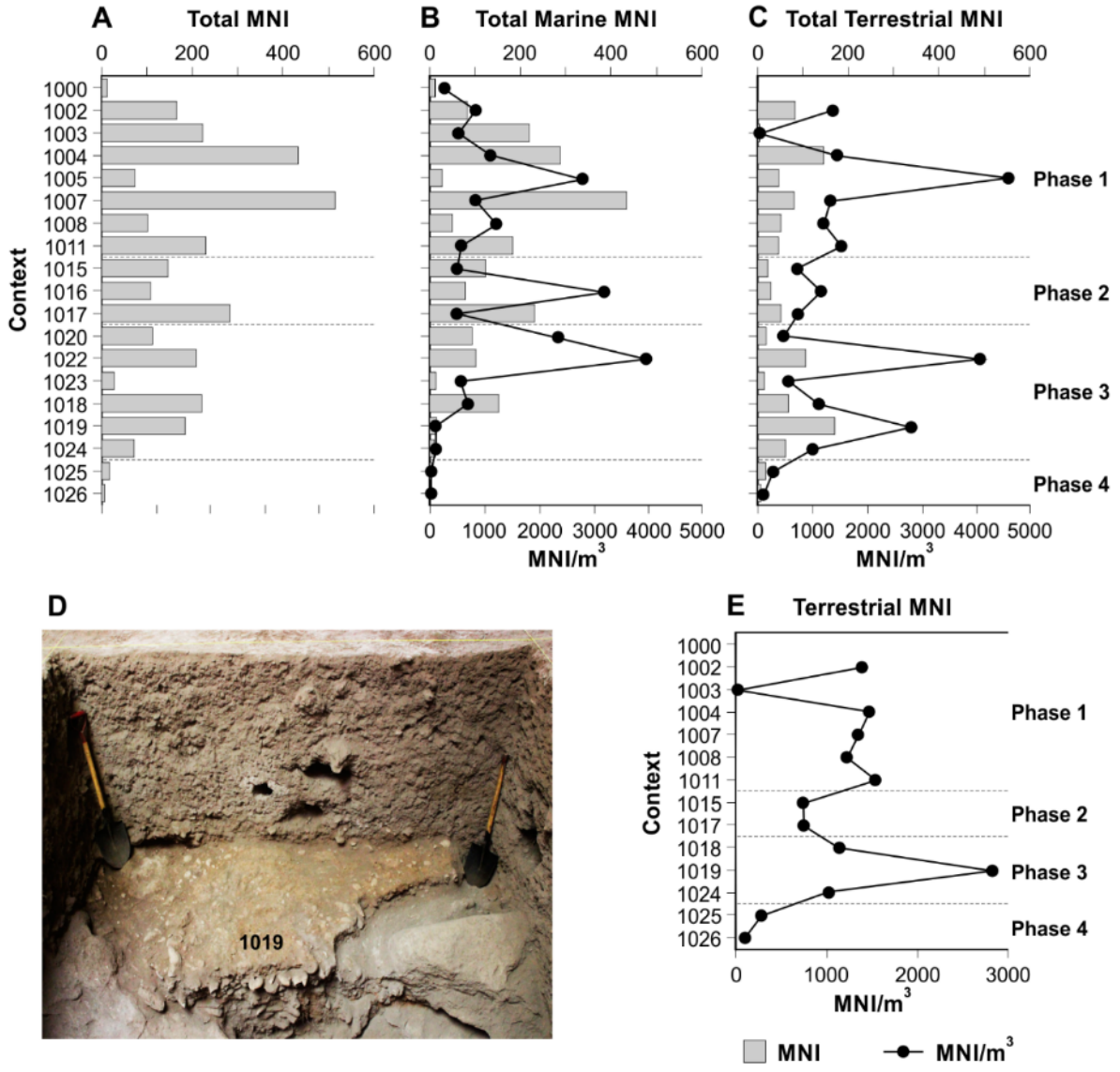


Figure 4: Relative abundance of all invertebrates by context (A), MNI and volume corrected MNI/m^3 for all marine (B) and terrestrial (C) invertebrates. The dense escargotière context (1019) is shown in (D), and the density of the terrestrial shell represented by MNI/m^3 is shown in (E) for the major contexts (with minor contexts 1005.1016, 1020, 1022, 1023 removed) to illustrate the significance of the *Achatina* spp. deposit in context 1019 (dashed lines indicate phase divisions).

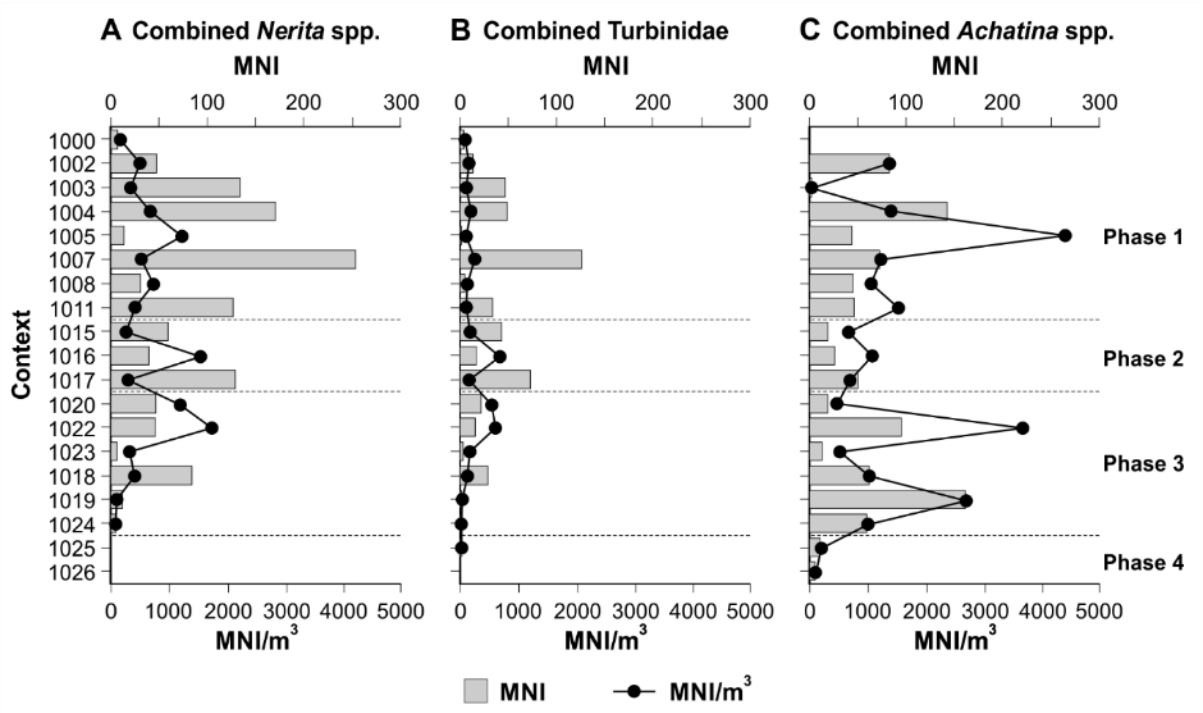


Figure 5: MNI and volume corrected MNI/m^3 by context for the combined *Nerita* spp. (A), Turbinidae (B) and *Achatina* spp. (C) taxonomic categories (note: different volume corrected scale for the Turbinidae) (dashed lines indicate phase divisions)

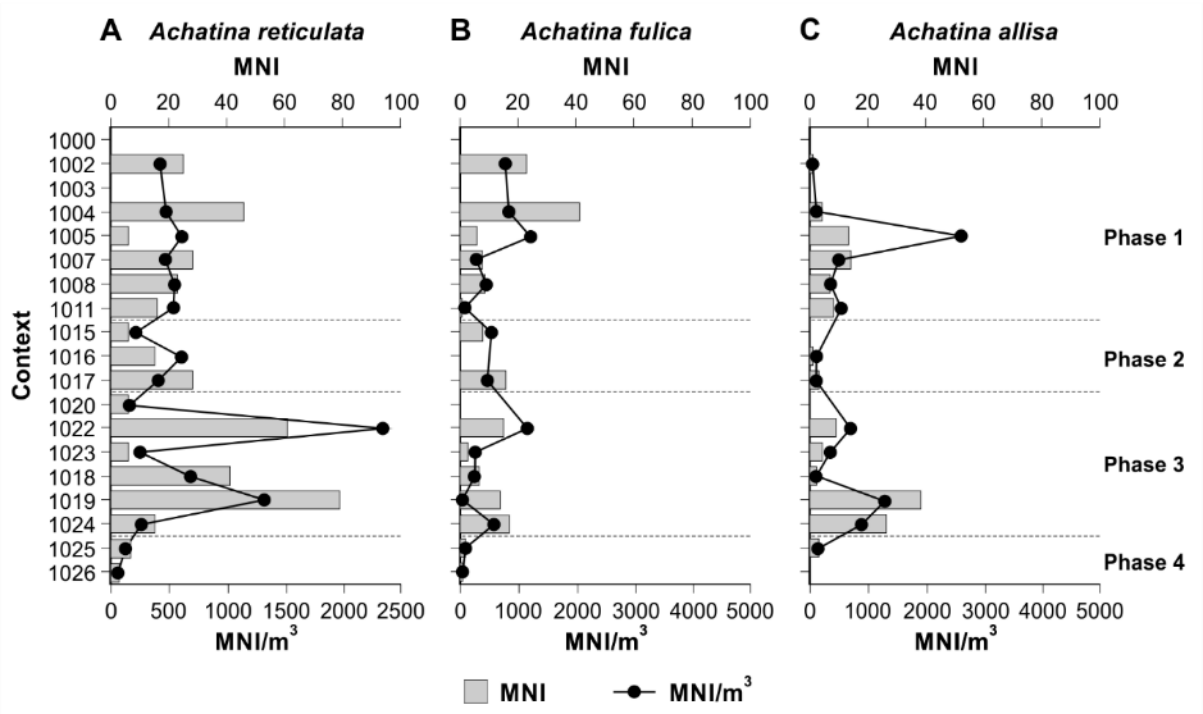


Figure 6: Relative abundance of *Achatina reticulata* (A), *Achatina fulica* (B) and *Achatina allisa* (C) per context by MNI and volume corrected MNI/m^3 (dashed lines indicate phase divisions)

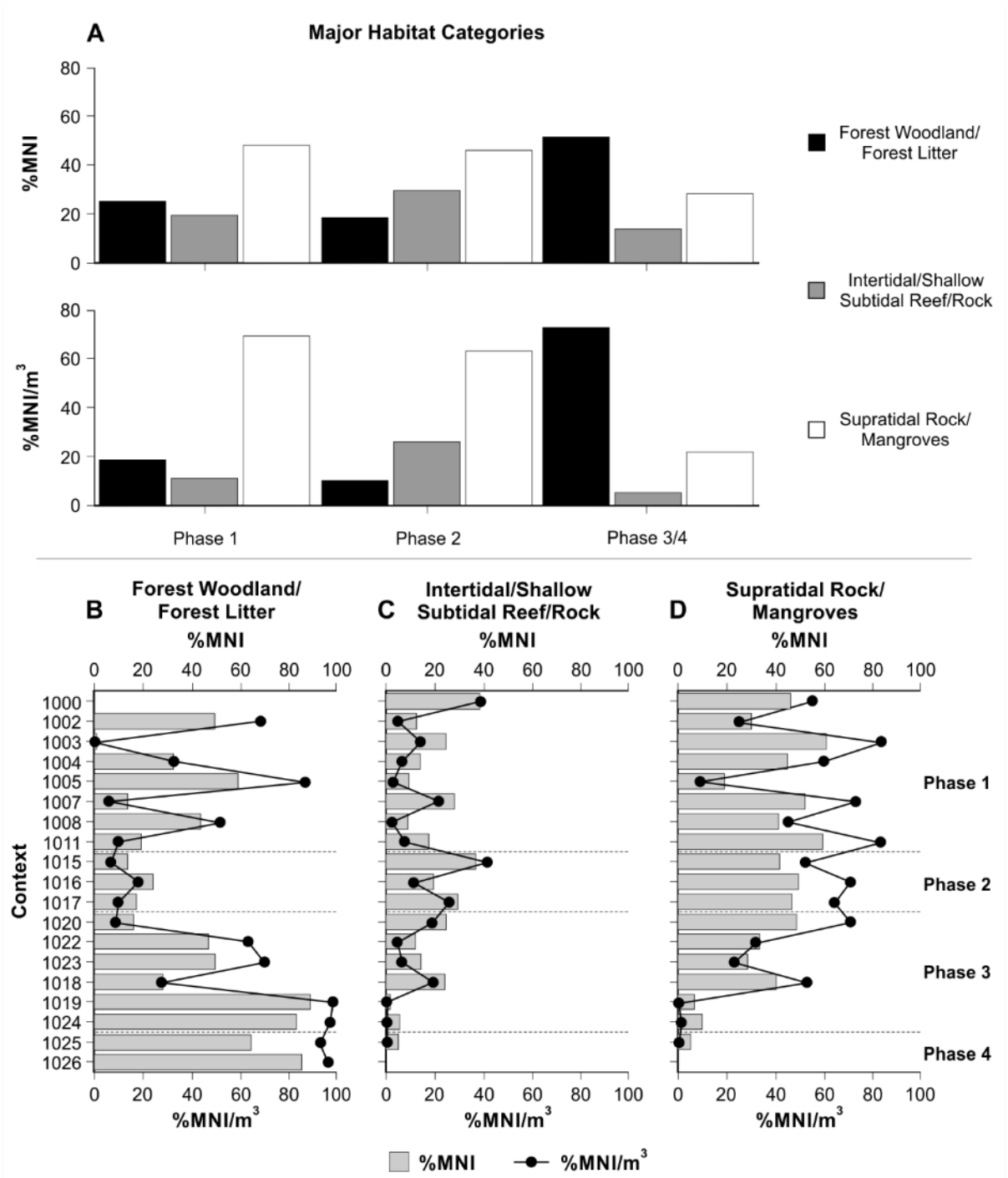


Figure 7: Relative abundance (%MNI and MNI/m^3) of habitat categories by Phase (A) and by context (B) forest woodland/forest litter (C) intertidal/shallow subtidal reef/rock (D) supratidal rock/mangroves (dashed lines indicate phase divisions)

A

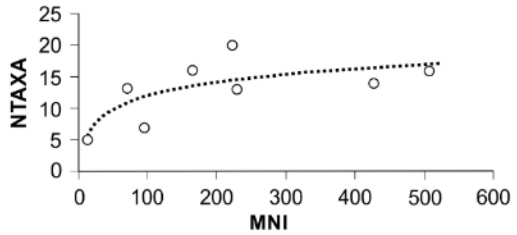
Taxon	Phase 1							
	1003	1002	1007	1004	1011	1005	1008	1000
NTAXA	**20**	**16**	**16**	**14**	**13**	**13**	**7**	**5**
Nerita spp.	133	47	252	169	126	12	30	6
Turbinidae	46	14	126	49	34	1	5	4
Cypraeidae	3	2	1	7	1	2	1	1
Achatina spp.	3	83	73	142	46	44	45	
Polyplacophora	1	3	16	25	10	2	12	
Strombidae	11	2	8	16	2	2		
Trochidae		1	14	2	3	2	2	
Terebralia palustris	1	2	1	2	1	1		
Muricidae	7	3	6	4	2			
Arcidae	2		1	1				1
Vasum spp.		1	2		1	1		
Cellana spp.	1		1	1				
Clypeomorus spp.	3	2		6				
Volema pyrum	1	1	2					
Angaria spp.	2			1				
Cerithium caeruleum	1		2					
Fasciolariidae				2			1	
Tectus spp.	1	2						
Echinoidea			1		1			
Littoraria spp.	1				1			
Ostreidae		1				1		
Ovula spp.	1				1			
Tellinidae		1				1		
Tonnidae	1					1		
Olividae								1
Conus spp.	2							
Euchelus spp.	2							
Atactodea spp.						1		
Cardiidae		1						
Veneridae			1					
Total MNI	**223**	**166**	**507**	**427**	**229**	**71**	**96**	**13**
T = 23.17°								

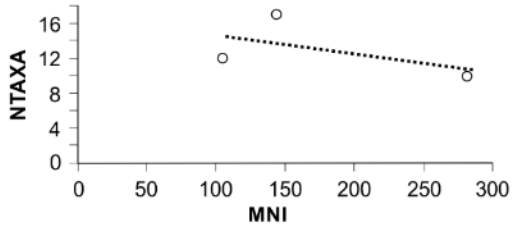
B

Taxon	Phase 2		
	1015	1016	1017
NTAXA	**17**	**12**	**10**
Nerita spp.	58	38	128
Strombidae	1	1	1
Turbinidae	43	17	73
Achatina spp.	20	27	50
Polyplacophora	1	15	4
Muricidae	3	1	13
Cypraeidae	4	1	8
Trochidae	3	1	2
Littoraria spp.	2	1	1
Echinoidea	1	1	
Terebralia palustris	1	1	
Tectus spp.	1		
Volema pyrum	2		
Angaria spp.	1		
Cerithium caeruleum	1		
Clypeomorus spp.		1	
Conus spp.	1		
Ostreidae	1		
Veneridae			1
Total MNI	**144**	**105**	**281**
T = 7.95°			

C

Taxon	Phase 3/4							
	1018	1020	1022	1023	1024	1019	1025	1026
NTAXA	**13**	**13**	**11**	**6**	**6**	**5**	**4**	**2**
Achatina spp.	62	19	95	13	59	161	12	6
Turbinidae	29	22	16	4	3	2	1	
Nerita spp.	83	47	45	7	5	12		
Polyplacophora	6	7	25	1	1		1	
Cypraeidae	5	2	3		1	1		
Muricidae	4	1	2	1				1
Trochidae	16	3	4					
Atactodea spp.	4	5					1	
Ostreidae		1	1					
Clypeomorus spp.	1		1					
Terebralia palustris		1	1					
Tectus spp.	1							
Arcidae		1						
Bursidae				1				
Strombidae			4					
Cardiidae		1						
Conus spp.	1							
Echinoidea	1							
Littoraria spp.		1						
Patella spp.					1			
Pteriidae	1							
Veneridae						1		
Total MNI	**214**	**111**	**197**	**27**	**70**	**177**	**15**	**7**
T = 19.89°								





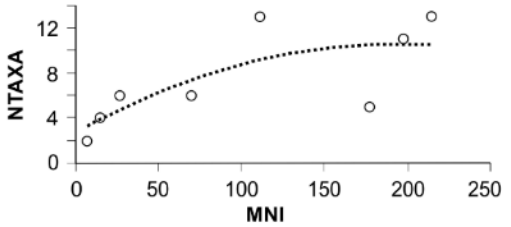


Figure 8: Kuumbi Cave nestedness matrices and species area curves for Phase 1 (A), Phase 2 (B) and combined Phases 3 and 4 (C)

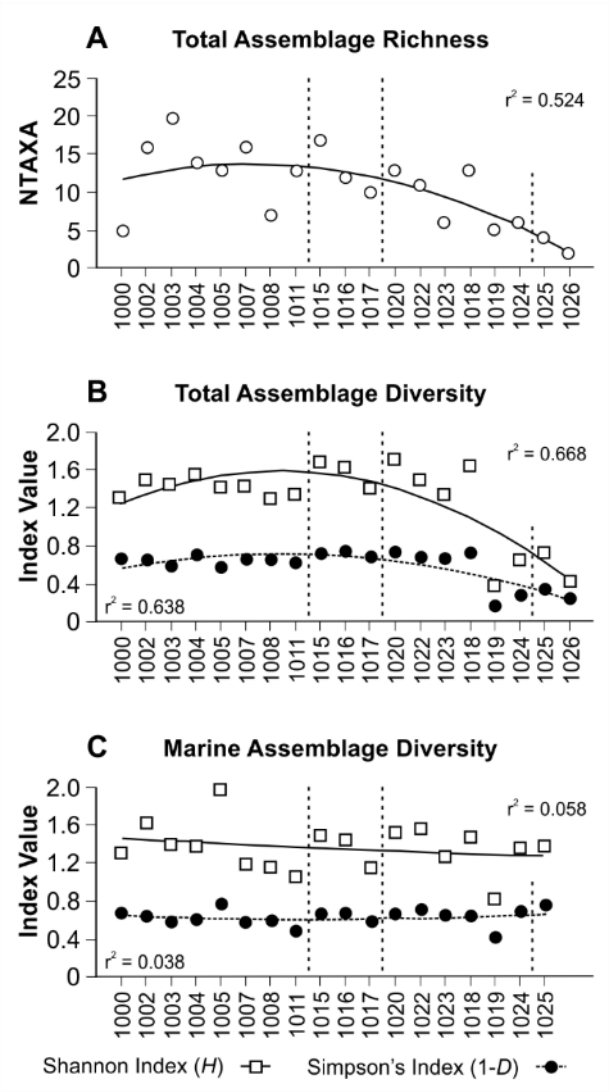


Figure 9: NTAXA (A), Shannon Index (B) and Simpson's Index (C) results (dashed lines indicate phase divisions; best fit second-order polynomial trend lines for visual comparison)

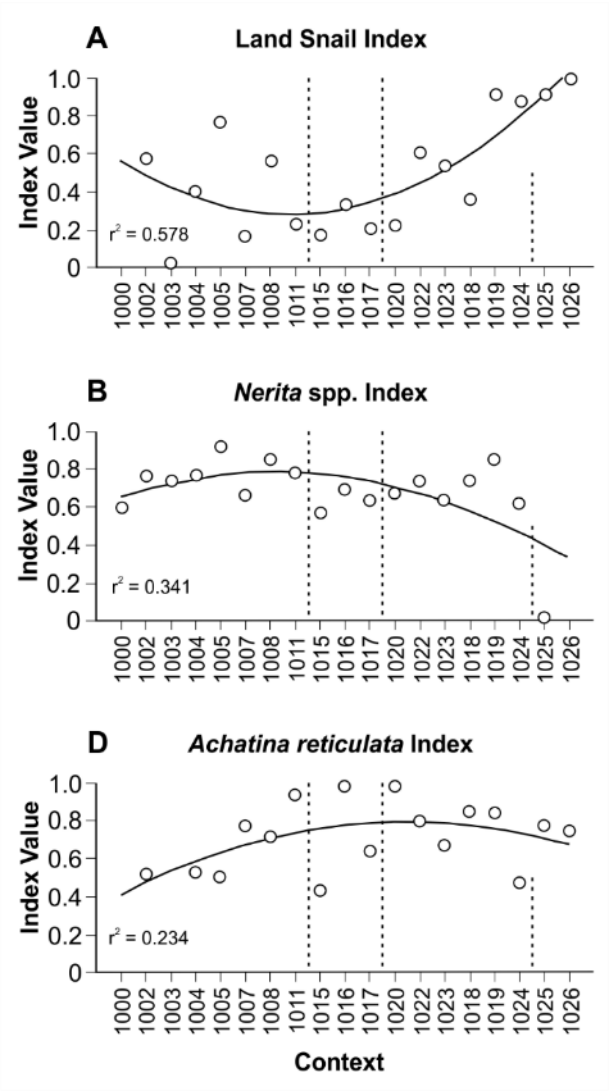


Figure 10: Land Snail index (A), *Nerita* spp. index (B) and *Achatina reticulata* index (C)

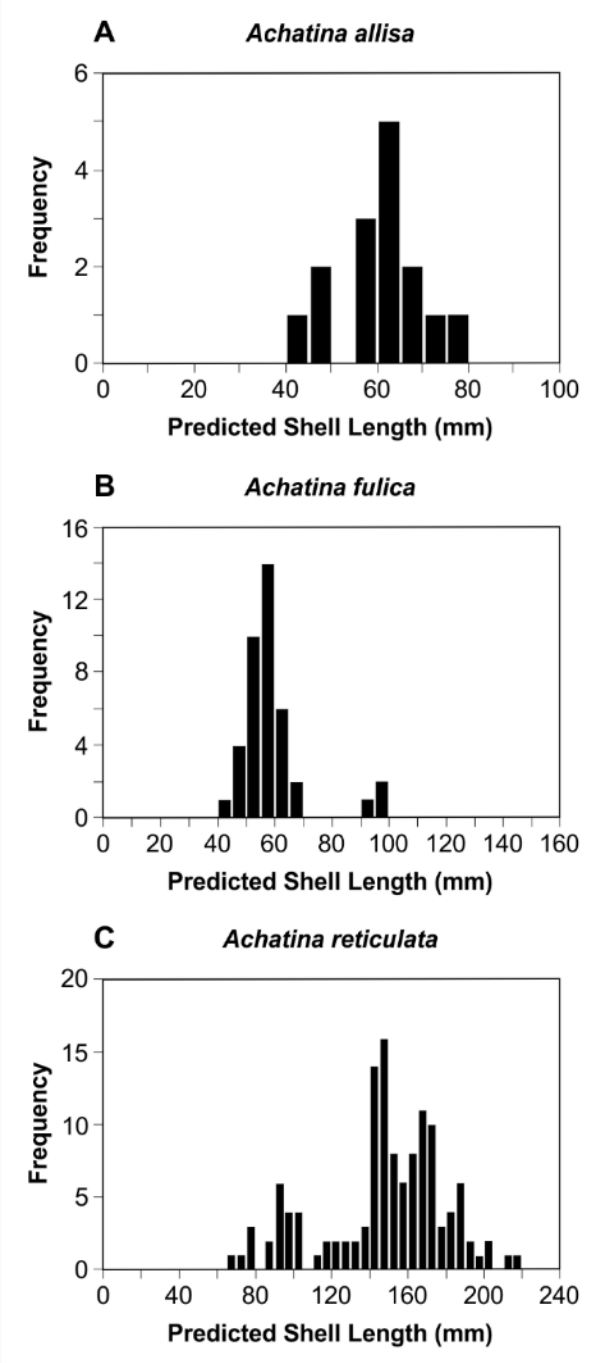


Figure 11: Total assemblage predicted shell length size frequency distributions for *Achatina allisa* (A), *Achatina fulica* (B) and *Achatina reticulata* (C)

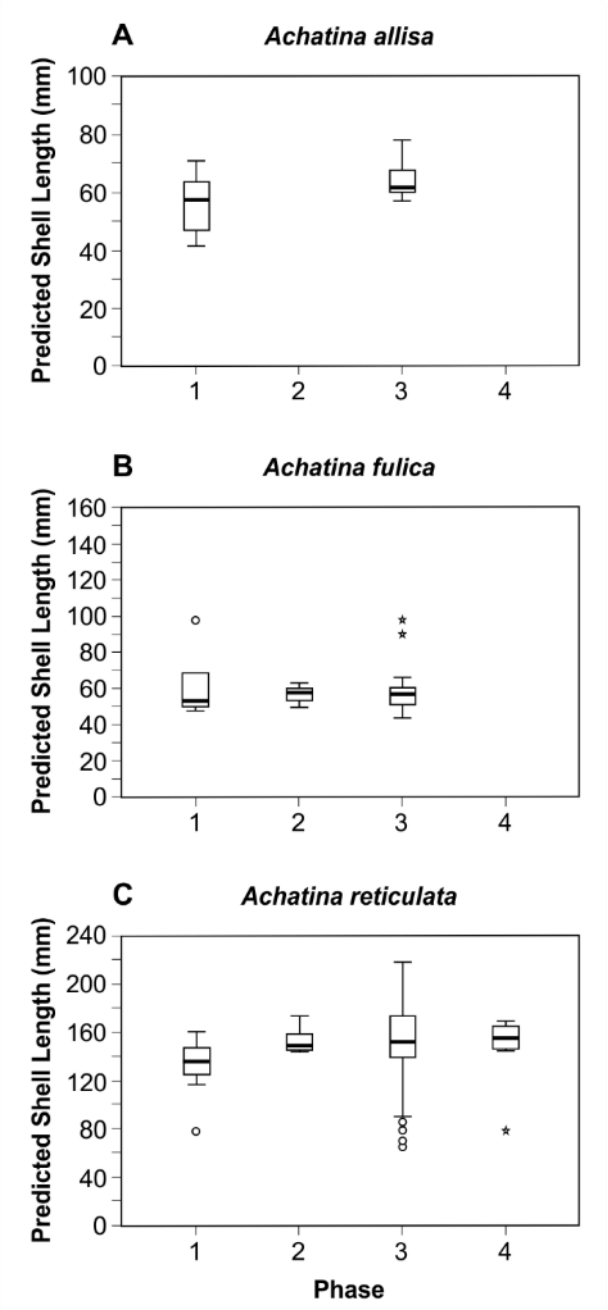


Figure 12: Predicted shell length boxplots by phase for *Achatina allisa* (A), *Achatina fulica* (B) and *Achatina reticulata* (C)

Tables

Table 1: Kuumbi Cave phase, context and sample volumes for the analytical units used in the following analyses with associated ages (following Prendergast et al. 2016 and Shipton et al. 2016)

Phase	Context	Combined Contexts	Total Context Volume (L)	Flotation Sample Volume (L)	Calibrated Age (cal BP)
1	1001	1000; 1001	50	50	
	1002		100	60	
	1003		435	120	640-540
	1004	1004; 1004B; 1010; 1004C	260	100	
	1005		10	10	
	1007		525	60	1485-1235; 770-600
	1008	1008; 1013; 1012	42	42	
	1011		320	30	1040-880; 1370-1300
2	1015		250	30	12620-12410
	1016		25	25	11750-11340
	1017		480	70	13040-12790; 12640-12420
3	1020		40	40	
	1022	1021; 1022	26	26	
	1023		25	25	
	1018		220	60	
	1019		180	60	18830-18555
	1024		120	60	
4	1025		240	60	20240-19880
	1026		570	60	

Table 2: Achatinidae independent control sample structure and descriptive statistics, data obtained from Bequaert 1951 (87, 127, 135) and the Zanzibar and Pemba collections in the Department of Natural Sciences, National Museum of Wales

Achatina allisa	**No.**	**Mean**	**SD**	**Min**	**Max**	**Skew**	**Kurtosis**
Shell Length	25	61.12	18.71	14.4	92.0	-0.938	0.986
Columella Length	21	55.33	18.23	13.0	86.5	-0.795	0.624
Shell Width	25	30.24	7.46	11.0	42.0	-1.064	1.097
Body Whorl Width	21	23.45	5.91	8.5	32.0	-1.078	0.966
Aperture Length	25	32.72	8.97	9.5	45.0	-1.102	1.175
Aperture Width	25	16.04	4.14	5.5	22.0	-0.868	0.628
Achatina fulica							
Shell Length	25	84.38	31.51	26.5	134.0	-0.296	-0.831
Columella Length	17	72.03	32.03	25.0	129.0	0.217	-0.878
Shell Width	25	44.28	15.12	12.5	66.0	-0.641	-0.373
Body Whorl Width	17	32.12	13.15	11.5	52.0	0.007	-1.182
Aperture Length	25	46.18	16.14	12.0	67.5	-0.712	-0.283
Aperture Width	25	24.06	8.72	6.0	38.0	-0.541	-0.384
Achatina reticulata							
Shell Length	28	121.84	59.34	12.5	194.0	-0.602	-1.182
Columella Length	13	75.12	59.92	11.5	185.0	0.998	-0.443
Shell Width	28	57.13	24.21	8.5	87.0	-0.688	-0.923
Body Whorl Width	13	32.31	20.37	7.5	67.0	0.738	-0.86
Aperture Length	28	58.57	25.75	7.5	90.0	-0.722	-0.977
Aperture Width	28	29.29	12.19	4.5	43.5	-0.738	-0.903

Table 3: Correlation, regression and significance test results for predicting log shell length from the Achatinidae independent control sample log-transformed measurement data

	Pearson Correlation		Linear Regression			ANOVA		
Achatina allisa	***r***	***p***	r^2	***A***	***b***	***F***	**df**	***p***
Columella Length	0.999	<0.001	0.997	0.074042	0.970392	6625.199	1	<0.001
Shell Width	0.987	<0.001	0.975	-0.217446	1.348824	896.276	1	<0.001
Body Whorl Width	0.992	<0.001	0.984	-0.129705	1.377048	1164.808	1	<0.001
Aperture Length	0.989	<0.001	0.978	0.051890	1.142535	1004.363	1	<0.001
Aperture Width	0.980	<0.001	0.960	0.220594	1.294164	553.483	1	<0.001
Achatina fulica	***r***	***p***	r^2	***A***	***b***	***F***	**df**	***p***
Columella Length	0.999	<0.001	0.999	0.044168	0.988961	13145.943	1	<0.001
Shell Width	0.986	<0.001	0.971	0.263397	1.008218	778.164	1	<0.001
Body Whorl Width	0.990	<0.001	0.980	0.294487	1.050544	749.296	1	<0.001
Aperture Length	0.981	<0.001	0.962	0.349910	0.945770	578.821	1	<0.001
Aperture Width	0.981	<0.001	0.962	0.641408	0.929357	575.452	1	<0.001
Achatina reticulata	***r***	***p***	r^2	***A***	***b***	***F***	**df**	***p***
Columella Length	1.000	<0.001	0.999	0.061853	0.981539	18187.027	1	<0.001
Shell Width	0.995	<0.001	0.990	-0.069204	1.219259	2708.017	1	<0.001
Body Whorl Width	0.998	<0.001	0.996	0.004065	1.240328	2643.218	1	<0.001
Aperture Length	0.997	<0.001	0.994	0.062797	1.139167	4514.429	1	<0.001
Aperture Width	0.993	<0.001	0.987	0.247272	1.243783	1964.685	1	<0.001

Table 4: Invertebrate taxonomic categories, sample MNI and total assemblage MNI

		Phase 1							Phase 2						Phase 3					Phase 4		Total
Class/Family	**Taxon**	**1000**	**1002**	**1003**	**1004**	**1005**	**1007**	**1008**	**1011**	**1015**	**1016**	**1017**	**1020**	**1022**	**1023**	**1018**	**1019**	**1024**	**1025**	**1026**	**MNI**
Bivalvia (Marine)																					
Arcidae	Arcidae				1																**1**
	Anadara antiquata	1		1			1						1								**4**
	Barbatia spp.			1																	**1**
Cardiidae	Cardiidae												1								**1**
	Tridacninae spp.		1																		**1**
Mesodesmatidae	*Atactodea* spp.																		1		**1**
	Atactodea spp. (Juvenile)												1								**1**
	Atactodea striata					1							5			4					**10**
Ostreidae	Ostreidae		1			1				1			1	1							**5**
Pteriidae	Pteriidae															1					**1**
Tellinidae	Tellinidae		1			1															**2**
Veneridae	Veneridae											1									**1**
	Dosinia spp.																1				**1**
	Gafrarium spp.						1														**1**
Gastropoda (Marine)																					
Angariidae	*Angaria* spp.			2						1											**3**
	Angaria delphinus				1																**1**
Bursidae	Bursidae														1						**1**
Cerithiidae	*Cerithium caeruleum*			1			2			1											**4**
	Clypeomorus spp.		2	3	6						1			1		1					**14**
Chilodontidae	*Euchelus* spp.			2																	**2**
Conidae	*Conus* spp.			2						1											**3**
	Conus ebraeus															1					**1**
Cypraeidae	Cypraeidae				1											1					**2**
Cypraeidae	*Cypraea* spp.	1	2		3		1	1		1		8	2	2		3	1				**25**
	Cypraea tigris			3	2	1			1	3	1			1		1		1			**14**
	Mauritia spp.				1	1															**2**
Fasciolariidae	Fasciolariidae				1			1													**2**
	Pleuroploca trapezium				1																**1**
Fissurelidae	Fissurellidae															1					**1**
Hipponicidae	*Hipponix* spp.				1				1		2	1		1							**6**
Littorinidae	*Littoraria* spp.			1					1	2	1	1	1								**7**

		Phase 1								Phase 2					Phase 3					Phase 4		Total
Class/Family	**Taxon**	**1000**	**1002**	**1003**	**1004**	**1005**	**1007**	**1008**	**1011**	**1015**	**1016**	**1017**	**1020**	**1022**	**1023**	**1018**	**1019**	**1024**	**1025**	**1026**	**MNI**
Melongenidae	*Volema pyrum*		1	1			2			2											**6**
Muricidae	Muricidae		1		1							1								1	**4**
	Mancinella spp.									1		4		1							**6**
	Mancinella armigera		1	7	3		5		1	2		7									**26**
	Reishia clavigera											1				3					**4**
	Thais spp.		1				1		1		1		1	1	1	1					**8**
Nacellidae	*Cellana* spp.			1	1		1														**3**
Neritidae	*Nerita* spp.			1	9		2		1		1	3	1	3		1					**20**
	Nerita albicilla	1	7	28	34	1	41	5	22	10		11		2		7					**169**
	Nerita balteata	1	19	64	55	4	115	7	49	13	11	41	3	11		34	2				**429**
	Nerita exuvia						3	1		2											**6**
	Nerita plicata	1	6	7	32	2	36	7	27	21	14	46	23	12	6	8	1	1			**250**
	Nerita polita		8	20	17		20	3	10	2	3	4	1	6		21					**115**
	Nerita textilis	2	7	13	21	5	35	7	17	10	9	20	19	11	1	11	9	4			**201**
	Nerita undata	1			1							3				1					**6**
Olividae	Olividae	1																			**1**
Ovulidae	*Ovula* spp.								1												**1**
Ovulidae	*Ovula ovum*			1																	**1**
Patellidae	*Patella* spp.																	1			**1**
Potamididae	*Terebralia palustris*		2	1	2	1	1		1	1	1		1	1							**12**
Strombidae	Strombidae						1														**1**
	Gibberulus gibberulus		1	8	8	2	1							2							**22**
	Strombus spp.		1	3	8		6		2	1	1	1		2							**25**
Tegulidae	*Tectus* spp.															1					**1**
Tegulidae	*Tectus pyramis*		2	1						1											**4**
Tonnidae	Tonnidae			1		1															**2**
Trochidae	Trochidae		1			1						1				1					**4**
	Monodonta spp.				2			1		1	1	1	1	2							**9**
	Monodonta labio					1	14	1	3	2			2	2		15					**40**
Turbinellidae	*Vasum* spp.								1												**1**
	Vasum rhinoceros		1			1	2														**4**
Turbinidae	Turbinidae		3					1										2			**6**
	Lunella coronata		5	18	20	1	23	3	10	5		6	1	2		29					**123**
	Turbo spp.	2			8				2	11	6	14	3	2	3		1		1		**53**
	Turbo argyrostomus						1														**1**

		Phase 1									Phase 2					Phase 3					Phase 4		Total
Class/Family	**Taxon**	**1000**	**1002**	**1003**	**1004**	**1005**	**1007**	**1008**	**1011**	**1015**	**1016**	**1017**	**1020**	**1022**	**1023**	**1018**	**1019**	**1024**	**1025**	**1026**	**MNI**
	Turbo setosus	2	6	28	21		102	1	22	27	11	53	18	12	1		1	1			**306**
Gastropoda (Terrestrial)																					
Achatinidae	*Achatina* spp.		34	3	51	19	23	6	21	6	11	3	13	10		12	30	1		2	**245**
	Achatina spp. (Juvenile)											1			1	2	2	1	1		**8**
	Achatina allisa		1		4	13	14	7	8		1	3		9	4	2	38	26	3		**133**
	Achatina allisa (Juvenile)				1												2				**3**
	Achatina fulica agg.		23		41	6	8	9	1	8		16		15	3	7	14	17	2	1	**171**
	Achatina fulica agg. (Juvenile)				1		1			1				4							**7**
	Achatina reticulata		25		46	6	28	23	16	6	15	28	6	61	6	41	79	15	7	3	**411**
Maizaniidae	*Maizania zanzibarica*										2	1		1		2					**6**
Pomatiasidae	*Tropidophora zanguebarica*				2		6	6		1				6		2	3		2		**28**
Streptaxidae	*Edentulina obesa*																		1		**1**
	Edentulina ovoidea																		1		**1**
Subulinidae	*Homorus* (*Subulona*) *usagarica*																1				**1**
	Pseudoglessula subolivacea agg.					2												1			**3**
Polyplacophora	Polyplacophora		3	1	25	2	16	12	10	1	15	4	7	25	1	6		1	1		**130**
Hexanauplia	Cirripedia				1																**1**
Malacostraca	Decapoda				1	1	1						1								**4**
Echinodermata	Echinoidea						1		1	1	1					1					**5**
Total MNI		**13**	**166**	**223**	**434**	**74**	**515**	**102**	**230**	**146**	**109**	**284**	**113**	**209**	**28**	**221**	**185**	**72**	**20**	**7**	**3151**
No. Taxonomic Categories		**10**	**28**	**28**	**37**	**23**	**33**	**19**	**25**	**31**	**21**	**28**	**23**	**29**	**11**	**30**	**15**	**13**	**10**	**4**	
Total Context Volume (L)		**50**	**100**	**435**	**260**	**10**	**525**	**42**	**320**	**250**	**25**	**480**	**40**	**26**	**25**	**220**	**180**	**120**	**240**	**570**	
Context Flotation Sample (L)		**50**	**60**	**120**	**100**	**10**	**60**	**42**	**30**	**30**	**25**	**70**	**40**	**26**	**25**	**60**	**60**	**60**	**60**	**60**	

Table 5 Chi-Squared adjusted residuals for Kuumbi Cave habitat categories (* = significantly lower MNI per habitat category; ** = significantly greater MNI per habitat category)

Habitat Category	Phase 1	Phase 2	Phase 3/4
Forest Woodland / Forest Litter	**15.122****	**-6.984***	**-8.244***
Forest / Scrub	**2.306****	-1.910	-0.616
Forest Vegetation	1.629	1.085	**-2.280***
Forest Vegetation/Forest Litter	2.318	-0.643	-1.588
Intertidal Rock/Mangrove	-0.817	-0.040	0.762
Intertidal/Shallow Subtidal Reef / Rock	**-5.062**	**6.301****	-0.245
Intertidal / Shallow Subtidal Sand/Mud	-1.558	-0.294	1.618
Intertidal / Shallow Subtidal Seagrass	-1.496	1.057	0.538
Intertidal / Subtidal Various	-0.508	0.243	0.270
Subtidal Reef / Rock	-0.508	-0.598	0.908
Supratidal Rock/Mangrove	**-9.833***	1.814	**7.428****

Table 6: Kuumbi Cave sample size (MNI), richness (NTAXA), diversity and proportional index results by context (note: for marine taxa contexts 1025 and 1026 are combined)

		Total Assemblage				Marine Taxa						
Phase	**Context**	**MNI**	**NTAXA**	***H***	**1-*D***	**MNI**	**NTAXA**	***H***	**1-*D***	**Land Snail Index**	***Nerita* Index**	***Achatina reticulata* Index**
1	1000	13	5	1.31	0.67	13	5	1.31	0.67	--	0.60	--
	1002	166	16	1.51	0.66	83	15	1.63	0.65	0.58	0.77	0.52
	1003	223	20	1.45	0.60	220	19	1.40	0.59	0.02	0.74	--
	1004	427	14	1.56	0.71	285	13	1.38	0.61	0.39	0.78	0.53
	1005	71	13	1.42	0.58	27	12	1.99	0.77	0.77	0.92	0.50
	1007	507	16	1.44	0.67	434	15	1.20	0.58	0.16	0.67	0.78
	1008	96	7	1.31	0.63	51	6	1.16	0.59	0.56	0.86	0.72
	1011	229	13	1.35	0.73	183	12	1.07	0.49	0.22	0.79	0.94
2	1015	144	17	1.69	0.76	124	16	1.50	0.66	0.17	0.57	0.43
	1016	105	12	1.64	0.69	78	11	1.45	0.68	0.33	0.69	1.00
	1017	281	10	1.42	0.76	231	9	1.15	0.59	0.20	0.64	0.64
3	1020	111	13	1.73	0.75	92	12	1.53	0.67	0.22	0.68	1.00
	1022	197	11	1.50	0.69	102	10	1.57	0.72	0.61	0.74	0.80
	1023	27	6	1.35	0.68	14	5	1.27	0.65	0.54	0.64	0.67
	1018	214	13	1.65	0.74	152	12	1.48	0.65	0.36	0.74	0.85
	1019	177	5	0.38	0.17	16	4	0.82	0.41	0.92	0.86	0.85
	1024	70	6	0.65	0.28	11	5	1.37	0.69	0.88	0.63	0.47
4	1025	15	4	0.72	0.35	4	4	1.39	0.75	0.92	0.00	0.78
	1026	7	2	0.41	0.25					1.00	--	0.75

Table 7: Total sample and Phase descriptive statistics for *A. allisa*, *A. fulica* and *A. reticulata* predicted shell lengths

Achatina allisa	**No.**	**%MNI**	**Mean**	**Median**	**Mode**	**SD**	**Min**	**Max**	**Skew**	**Kurtosis**
Total Sample	15	11.28	60.41	61.54	41.57*	9.66	41.57	77.99	-0.40	0.19
Phase 1	7	14.89	55.97	57.49	41.57*	11.05	41.57	70.89	-0.05	-1.72
Phase 3	8	10.13	64.29	61.61	57.15*	6.72	57.15	77.99	1.34	1.65
Achatina fulica										
Total Sample	40	23.39	58.98	57.78	44.09*	12.30	44.09	98.85	2.10	4.90
Phase 1	6	6.82	62.44	53.89	48.41*	19.28	48.41	98.60	1.73	2.82
Phase 2	8	33.33	57.67	58.51	50.40*	4.86	50.40	63.71	-0.72	-0.51
Phase 3	26	46.43	58.58	57.40	44.09*	12.31	44.09	98.85	2.08	5.17
Achatina reticulata										
Total Sample	126	30.66	147.63	150.10	144.10*	32.10	65.73	218.58	-0.58	-0.05
Phase 1	14	9.72	133.78	136.37	78.20*	20.58	78.20	160.55	-1.46	3.30
Phase 2	8	16.33	153.05	148.96	144.10*	10.33	144.10	173.51	1.30	1.06
Phase 3	97	46.63	149.27	151.95	148.01	34.39	65.73	218.58	-0.59	-0.34
Phase 4	7	70.00	146.43	155.20	78.89*	31.30	78.89	169.17	-2.14	4.99

* Multiple modes exist. The smallest value is shown